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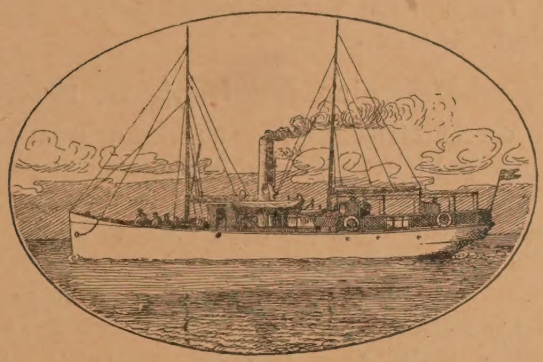
Report

of

The Danish Biological Station

to

The Board of Agriculture.



XXX.

1924.

By

C. G. Joh. Petersen,
Ph. D., L. L. D., D. Sc.
Director.

Copenhagen.
In Commission by G. E. C. Gad.
Centraltrykkeriet (C. Ferslew).
1925.

C. G. Joh. Petersen: Om de skalbærende Molluskers Udbredningsforhold i de danske Have indenfor Skagen 1888. 8°. 162 pg. 2 Kort.

Det videnskabelige Udbytte af Kanonbaaden »Hauch«s Togter i de danske Have indenfor Skagen. 1893. 4°. 464 pg. Atlas i folio.

Indhold: Echinodermata (Petersen), Diatomeer (Cleve), Undersøgelse af nogle Bundprøver (Rørdam), Mollusca (Petersen), Cephalopoda (Posselt), Crustacea malacostraca (Meinert), Hydrografi (Rørdam), Polyzoa (Levinsen), Ascidiæ simplices (Traustedt), Annulata, Hydroidæ, Anthozoa, Porifera (Levinsen), Nogle alm. Resultater (General Results, Engl.) (Petersen).

C. F. Drechsel: Oversigt over vore Saltvandsfiskerier med Kort og Planer. 1890. 4° 100 pg. Med et Tillæg: »Om Naturforholdene indenfor Skagen« af *C. G. Joh. Petersen*. Med Kort. 4°. 46 pg.

Fiskeri-Beretning for $18^{88}/_{89}$ til 1916.

Beretninger fra den danske biologiske Station findes paa dansk publiceret i de tilsvarende Fiskeri-Beretninger, til Beretning XXI med Tillæg. Senere udgives de som selvstændige Publicationer paa Dansk og paa Engelsk.

The Reports from The Danish Biological Station are also published in Danish in the corresponding Fiskeri-Beretning, until Report XXI with Appendix. Later on they are specially published in Danish and in English, but not in the Fiskeri-Beretning.

I. Fiskenes biologiske Forhold i Holbæk Fjord. (1890—91.*) 63 pg. Med et Kort.
II. Om vore Kutlingers *(Gobius)* Æg og Ynglemaade. (1891—92.) 9 pg. Med 2 Tavler.
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IV. On the Biology of our Flat-fishes and on the decrease of our Flat-fish Fisheries. (1893—94.) 146 pg. 2 Plates. 1 Chart. Many Tables.
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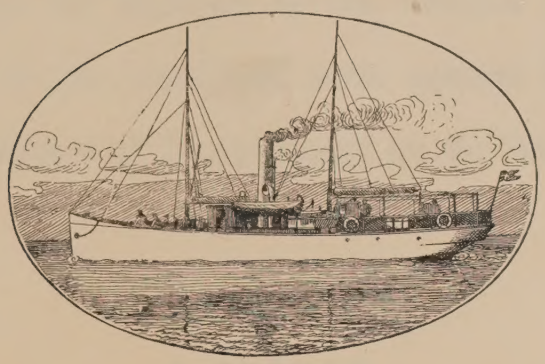

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Studies on the Biology of the Oyster *(Ostrea edulis)* in the Limfjord, with special Reference to the Influence of Temperature on the Sex Change.

By

R. SPÄRCK.

CONTENTS

	page
Preface	5
I. Summary of the Literature on Generation and Breeding Habits of the Oyster (*Ostrea edulis*)	7
II. Investigations on the Function of the Generative Organ of the Oyster	12
III. Influence of Surrounding Conditions on the Pelagic Larvæ	45
IV. Fluctuations in the Stock of Oysters in the Limfjord	50
V. Geographical Distribution of the Oyster	61
VI. Theoretical Importance of the Alternate Hermaphroditism	69
VII. Other Observations	72
VIII. Conclusions	79
Literature	81

PREFACE

In 1919, when I was engaged by the Danish Biological Station, I was given the task to investigate the biology of the oyster[1]) in the Limfjord, especially its breeding habits and the influence of the temperature on this latter. The present paper contains the results of some of these investigations. The first problem, which I wanted to solve, was whether the spawning proper was dependant on temperature or not. This necessitated a more detailed elucidation of the function of the reproductive organ of the oyster and the nature of its hermaphroditism, which thus became the principal subject of this paper. In connection with this I shall put forth my observations and experiences concerning the influence of temperature in other respects. I have further made an attempt to connect my interpretation of the breeding habits of the oyster, obtained through these investigations, with the quantitative fluctuations in the stock of oysters in the Limfjord, and with the geographic distribution of the European oyster in general. In the two last chapters I have finally mentioned the theoretic importance of the alternate hermaphroditism of the oyster, together with some other observations concerning its biology.

I take the opportunity here to express my best thanks to Dr. phil. C. G. Joh. Petersen, Director of the Danish Biological Station, for the interest with which he has followed my investigations, and for manifold help given in many different ways. I also want to thank Mr. Villars K. Lunn, Director of the Oyster Fishing Company, for his constant help in providing me with material for these investigations and assisting me on many other points, without his assistance I should not have been able to carry through this work. Finally I beg to express my gratitude to Professor, Dr. phil. Aug. Krogh for laboratory facilities in the Zoophysiological Laboratory of the University of Copenhagen and for helping me in the working out of some of my experiments there, also to the Lecturers C. M. Steenberg and M. Thomsen I am indebted for good advice, especially concerning the microscopic technique.

Copenhagen, Zool. Museum. March 1924.

R. SPÄRCK.

[1]) Here as anywhere in this paper where oysters are mentioned without any particular statement of species I speak of *O. edulis*, the only oyster species inhabiting Danish waters.

I.

Summary of the Literature on Generation and Breeding Habits of the Oyster (Ostrea edulis L.).

As might be expected when an animal, object of fishing, is concerned, the literature, both strictly scientific as well as more practical, contains many informations on the generation and breeding habits of *Ostrea edulis*. It is f. inst. since long ago a well known fact that there is a certain connection between the breeding habits of the oyster and the temperature, the geographical distribution of the oyster simply induces it. The authors who mention this connection and, on the whole, authors dealing with the breeding habits of the oyster most often confound two problems. When it is said that the spawning of the oyster has been good or bad in some locality in a certain year, it generally means that many or few young attached oysters have been found there, whilst, according to ordinary terminology, it would mean that the production of pelagic larvæ had been abundant or scarce. We have, therefore, in reality two problems to solve, one concerning generation, and another concerning the breeding habits till the young have fixed themselves.

Hoek (1883 p. 115) and Horst (1883 p. 257) have given a very complete account of the earlier literature, wherefore I shall be content to mention it in a short summary, and for the rest refer to the two said authors.

Already in 1690 Brach and in 1695 Leuwenhoek stated that the eggs of the oyster are after the spawning found between the shells of the mother animal where they are developing into larvæ which swim freely about for some time before attaching themselves. It is true that in the 18th and the first half of the 19th centuries the reproductive organs and breeding habits of the oyster are mentioned by different authors, but it is only in the latter half of the 19th century that these problems are made the object of thorough investigation. The first author who gave this subject particular attention was Davaine who published a series of papers (Davaine & Chaussat 1849, Davaine 1852 & 53).

in which he points out that among oysters we meet with individuals containing eggs as well as spermatozoa i. e. hermaphrodites, and at the same time others with respectively eggs or spermatozoa alone. This makes it easier to understand the discussion, so frequently occurring among earlier authors, whether the oyster be hermaphrodite or not. Davaine further demonstrates that individuals having produced spawn, immediately afterwards produce spermatozoa, and that the youngest individuals produce sperm; from this he draws the conclusion that an oyster first functions as a male and then as a female, and thereafter in the very same summer once more becomes a male. In a single case he even found an oyster with fry between the shells, which must have produced spawn in that particular summer, and which was now having ripe spermatozoa in the reproductive organs together with a commencing egg-development. According to Davaine, this individual should thus be going to produce spawn a second time in one summer. Davaine further states that it is one and the same organ which produces eggs as well as sperm, and he is of opinion that he has found the fecundation to take place in the sex organ proper; he supposes that the spermatozoa, developed during the male period, fertilize the eggs developing during the directly subsequent female period, so that it is self-fecundation which is taking place.

These opinions, concerning the sex organs of the oyster, were sharply criticised in the following years by Lacaze-Duthiers (1854 & 55). He thinks like Davaine that the oyster is a hermaphrodite, he acknowledges that some individuals appear in the form of males, some in the form of females, and finally also some containing both eggs and sperm. But he very fiercely attacks Davaine's interpretation of this fact as different successive stages, putting up against Davaine another explanation, to the effect that all individuals are to be regarded as being at a stage of hermaphroditism, and only differing in this that in most of the individuals the male, respectively the female, organ has been checked by the opposite organ, and that the two sexes are only in some few individuals equally developed. According to Lacaze-Duthiers, it is to be supposed that in each individual a sort of "struggle" for predominance is going on between the two sexes; in this he sees the explanation of Davaine's observation of sperm-development directly after spawning, he namely thinks that the chances for development of the male sex products are better after the sex organ has discharged its eggs. Lacaze-Duthiers thus must be of opinion that the spermatozoa have been present also in the apparently female stage, only hidden and checked by the female sex products, and therefore invisible or, at any rate, difficult to distinguish. In support of this perception Lacaze-Duthiers among other things maintains that he has succeeded — although after a very long time of searching — in finding a few spermatozoa in individuals in the female stage. He further puts up against Davaine that if a regular alternation from the male to the female stage and vice versa were going on, it would not be easy to find the explanation of the fact that the number of individuals in the male stage is always c. 100 times that of individuals in the female

stage, an observation which has been made by Davaine himself. As to the question of the fertilization the two authors do, however, agree, Lacaze-Duthiers also being of opinion that self-fecundation is taking place.

Finally Van Beneden (1855) has studied the function of the sex organs of the oyster. He completely adopts the perception of Davaine, and, in support of it, he maintains that, according to him, all oysters contain spermatozoa in the months from October to January, during which time he had examined a considerable number of oysters. As a result of these investigations he further puts forth that the spermatozoa, developed in the course of the summer, do not get into function until the following summer, so that there is no possibility of an oyster producing eggs two — or more — times in one and the same summer, such as Davaine was inclined to think.

About twenty years now passed before these questions were once more taken up for discussion in the zoological literature. Möbius in 1871 published a small paper on the propagation of *Ostrea edulis*, in which he presents ideas which are rather considerably deviating from those of earlier authors; he means to have stated that the oysters function during the breeding period either as males or as females, and that those having functioned as females sometimes afterwards produce spermatozoa. On the other hand, he denies the correctness of Lacaze-Duthier's observation — at any rate as far as the Sleswig oysters are concerned — to wit that also in the female stage some spermatozoa are present, and vice versa in the male stage some eggs; according to Möbius, self-fecundation is thus excluded. Möbius interprets the function of the generative organs in this way that he supposes all oysters to be neutral or sexless during the winter time, and that in the course of the spring the individuals develop either into males or females, and that these latter sometimes afterwards become males.

In the following years several small papers on this subject appeared. Gerbe (1876) substantiated that the oysters are even in their first year able to produce spawn, Gressy (1878) and Guérin (1897) both mention the oyster as a protandric hermaphrodite. Finally Robin (1880) mentions the hermaphroditism in oysters; from theoretical considerations he comes to the result that the opinions presented by Davaine, Lacaze-Duthiers and Van Beneden in explanation of the function of the sex organ in the oyster are hardly correct, but that this mollusc is certainly to be regarded as an ordinary protandric hermaphrodite.

The above mentioned works thus were present when Hoek in 1881—82 started his investigation of the structure and function of the generative organ of the oyster which makes out the foundation of the before mentioned work. Hoek's paper falls in two parts, a purely anatomical one and another about the function of the reproductive organ. Hoek here in the main adopts the opinion of the hermaphroditism of the oyster, as presented by Möbius, he namely states that ripe spermatozoa and eggs cannot be found at one time in one and the same individual, there would at any rate in such a case be only a very inconsiderable number

of the one sort. As to the question of an eventual alternation of male and female stages Hoek thinks that an oyster in one summer only occurs as a male or as a female; in order to explain the transitional stages, which he acknowledges to exist, he sets forth the supposition that the genital products of the oyster are developed one year before they enter into function, so that the eggs, which are developed later in the summer after the animal has functioned as a male, will not be ripe until the following summer. As for the rest, Hoek does not take up these facts for a more thorough discussion, regarding — as he says himself — the descriptive anatomy as the more essential part of his work, and he only mentions the question of the function of the generative organ quite en passant, at last.

Since the publication of Hoek's work hardly anything has appeared concerning the function of the reproductive organ of the oyster. Bourne (1890 p. 268) has published an account of Hoek's paper. Later on Hoek (1902 p. 61) has once more taken up the question and published a statistic investigation of the connection between the quantity of the contents of the intestine, the development of the generative organ, the weight of the individual a. s. f. He thinks that his investigation has confirmed the correctness of his conception from 1882, but does not, in this work either, enter into any details as to the function of the sex organ. Later on Dantan (1913 p. 871) has published a small communication in which he confirms Gerbe's statement that the oysters are able to produce eggs even in their first year, which had been denied by Lacaze-Duthiers; he further points out that the per-cent of individuals at the female stage increases with the age of the oyster to 20—25 %. These last years Orton (1921 a p. 500, 1921 b p. 586, 1922 p. 212) has treated these questions in a series of short communications; he has made several interesting observations as to at how young a stage the oyster may spawn, and once more substantiates that a change from the female to the male stage is going on. Finaly, the author of this paper has in a preliminary notice (Spärck 1922 p. 480) setl forth some of the views treated in this paper.

Besides the above named works, in which the structure and function of the reproductive organ of *O. edulis L.* are discussed, a certain number of papers treating the reproductive organs of *O. angulata* Lam. (Bouchon-Brandely 1882) and of *O. virginica* Gmel. (Brooks 1880 a. o.) have appeared; these papers are, however, of no special interest to the subject treated in this paper, the oyster species in question having separate sexes. On the other hand, a few papers discussing the propagation of *O. lurida* Crptr. from the pacific coast of North America are of some importance. In 1892 Ryder and Schieldt (1892 p. 352) published a very short communication to the effect that *O. lurida* is a hermaphrodite, and that the larvæ are during the first time of their lives to be found between the shells of the mother animal; as in *O. edulis* the eggs and the spermatozoa are developed in the same follicles. Later on Washburn (1899 p. 478) has made the structure of the generative organ the object of a more thorough study. He is of opinion that he has found eggs and spermatozoa simultaneously in one and the same indivi-

dual, and further, in a few cases, eggs surrounded by ripe spermatozoa, wherefore he thinks himself justified in determining *O. lurida* as a self-fertilizing hermaphrodite. On the foundation of these observations Washburn further expresses his doubt as to the correctness of Möbius's ideas concerning the hermaphroditism of *O. edulis*, Washburn is evidently of opinion that in this respect *O. lurida* and *O. edulis* are homogeneous.[1])

Besides these works a certain number of papers concerning the pelagic spawn and its biology have appeared. They are, however, in the main containing purely descriptive and morphological studies, in which the surrounding conditions, indispensable for the thriving and growth of the larva, are only exceptionally discussed. Among such works we mention, as to the European oyster, Möbius (1877), Horst (1883) and Dantan (1916), as to the American oyster, Brooks (1880), Ryder (1883), Stafford (1909 & 1912) and Churchill (1921). The last named authors somewhat more specially study the influence of the surrounding conditions on the larva, the length of the pelagic stage, which Stafford states to be a month, and other similar circumstances. Special attention ought, however, to be called to the paper by Hagmeier (1916) who has thoroughly studied the influence of the temperature on the growth of the pelagic spawn, and who has proved, through a series of investigations performed in a tank on Sild at the west coast of Sleswig, that the growth-rate is very much increased according to the temperature. During the later years similar investigations have been made by Mazzarelli (1922 p. 151), and, as to Japanese species, by Amemiya (1921 p. 159).

Besides the above named papers directly treating the breeding habits of the oyster, these questions are also mentioned in different works treating the oyster or oyster-fishing in general, f. inst. in C. G. Joh. Petersen (1907) who speaks of the influence of the temperature and the salinity on the pelagic spawn, and in the rather numerous papers discussing the Norwegian oyster basins (Helland-Hansen (1907) a. o.). The influence of the temperature on the generation is here frequently discussed, and it is stated that a high temperature causes an abundant yield of young oysters; any detailed elucidation of the kind of this influence is, however, not to be found in these papers.

Finally, several other zoological papers which are of interest in this connection ought to be mentioned, partly Pelseneer's paper on hermaphroditism in the molluscs (1894), in which he also mentions the hermaphroditic *Ostrea*-species, about the hermaphroditism of which he writes p. 23: "The question of sex in oysters has long been a subject of controversy, and its solution which presents decided

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[1]) Pelseneer (1911 p. 27) mentions a series of oyster species as having separate sexes. As we have to do with preserved specimens from an Expedition no conclusions can, however, with absolute certainty be drawn from this material. Recent Japanese investigations (Amemiya 1921 p. 150) prove *O. denselamellosa* Lischke to be a hermaphrodite, *O. gigas* Thunb. and *spinosa* Quoy as having separate sexes.

difficulties, is not yet universally recognized", partly Orton's paper on the influence of the temperature on the breeding habits of marine animals, among which also *Ostrea edulis* is mentioned (1920 p. 343); he expresses the opinion here that the oysters spawn when the temperature is beyond a certain limit, Orton means 15^0-16^0, and continues as long as the temperature keeps beyond this limit; according to this statement the duration of the spawning season should be the longer the further we go South.

From what has hitherto appeared in the literature about the breeding habits of the oyster we may take it for granted that this species is hermaphroditic, and further that the same individual in certain periods produces so to say exclusively eggs or spermatozoa; on the other hand, nothing definite is at hand concerning an eventual alternation between these stages, and especially nothing about the factors which are the conditions of this alternation. It is in consequence of this that *Ostrea edulis* is in the zoological textbooks (Claus, Boas) shortly designated as a hermaphrodite without any further statement as to the kind of hermaphroditism. It is therefore the author's intention in this investigation first to try to find out the kind of hermaphroditism of the oyster, further to examine whether surrounding conditions, especially the temperature, are of any influence to the developing and duration of the different stages, or whether the so often mentioned and quite indubitable influence of the temperature on the rise of an abundant stock of young fixed oysters is exclusively due to the influence of the temperature on the pelagic spawn, stated by Hagmeier.

II.

Investigations on the Function of the Generative Organ of the Oyster.

In order to have this question settled I have applied the method, through observations in the nature and examination of a rather considerable material to form an opinion of the solving of the problem, and then to have the eventual correctness of this opinion further tested through different experiments. The first part of the investigation mainly took place from May 1919 to July 1921, during which time I examined the generative organ in 1400 oysters originating from a series of localities in the various parts of the Limfjord, so that oysters from the same place have been examined at different seasons. Samples comprising 20–60 individuals from each locality have been examined at different times of the year.

1919

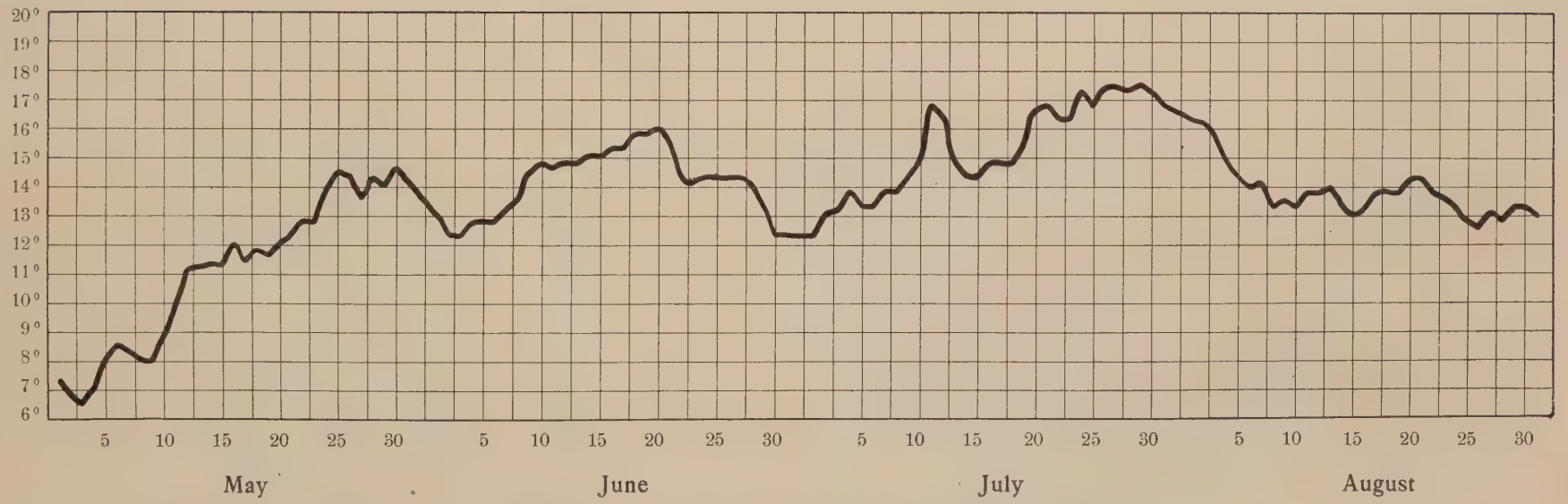

Fig. 1. Surface temperature at 8 a. m. at Oddesund.

1920

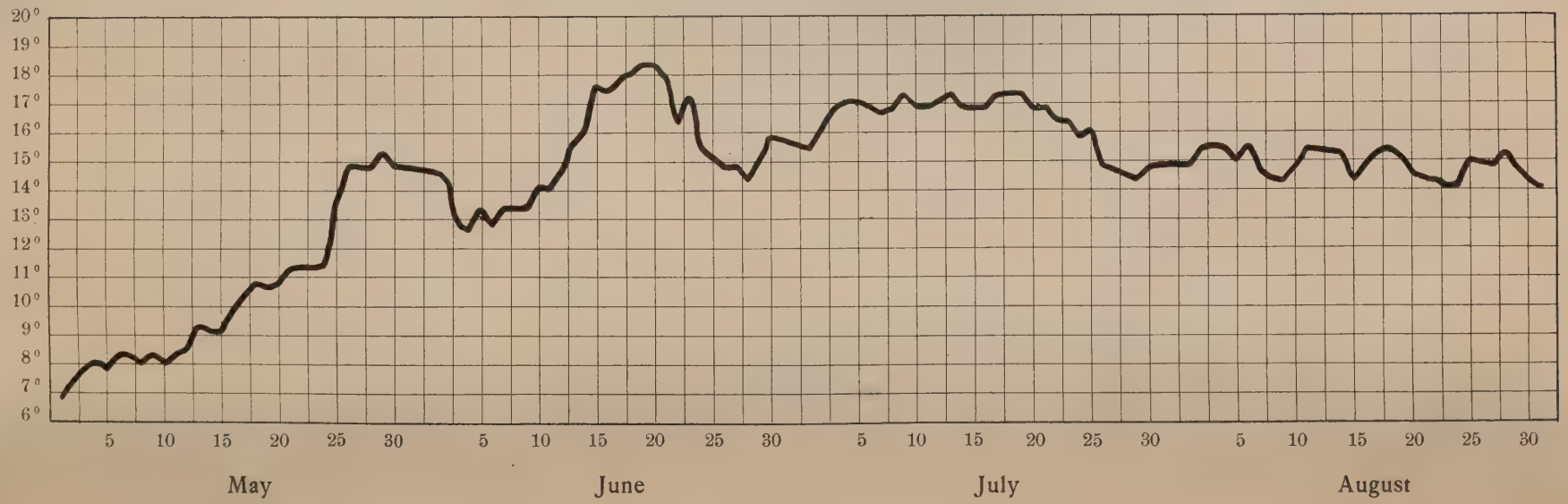

Fig. 2. Surface temperature at 8 a. m. at Oddesund.

1921

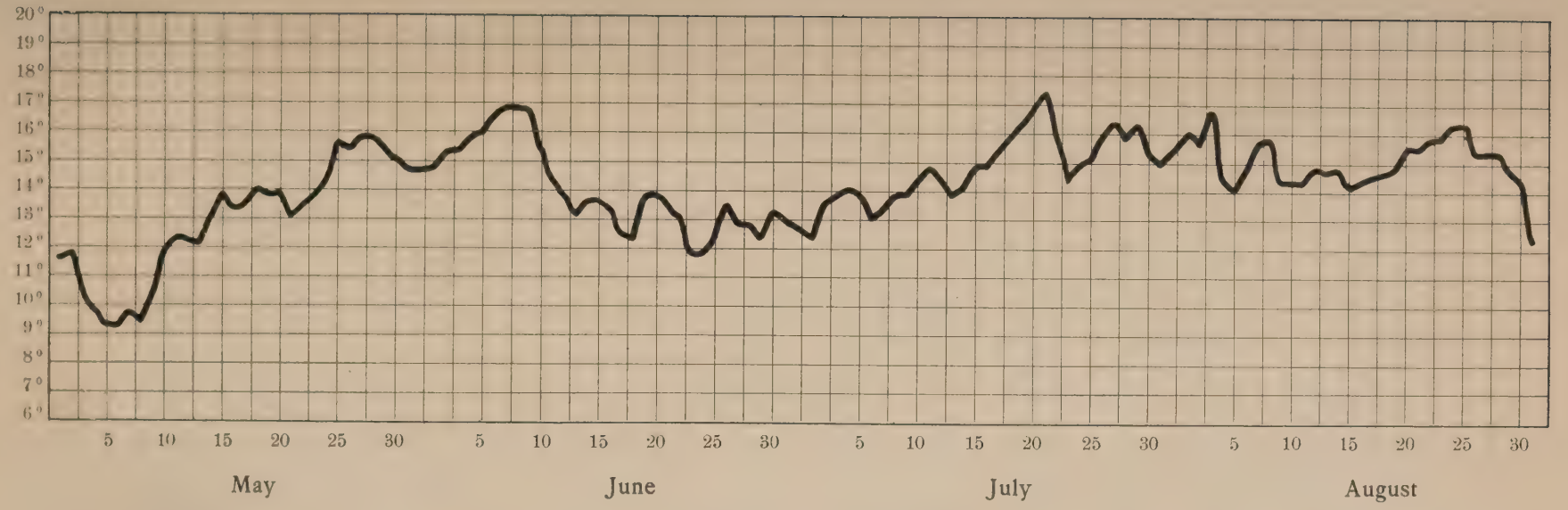

Fig. 3. Surface temperature at 8 a. m. at Oddesund.

1923

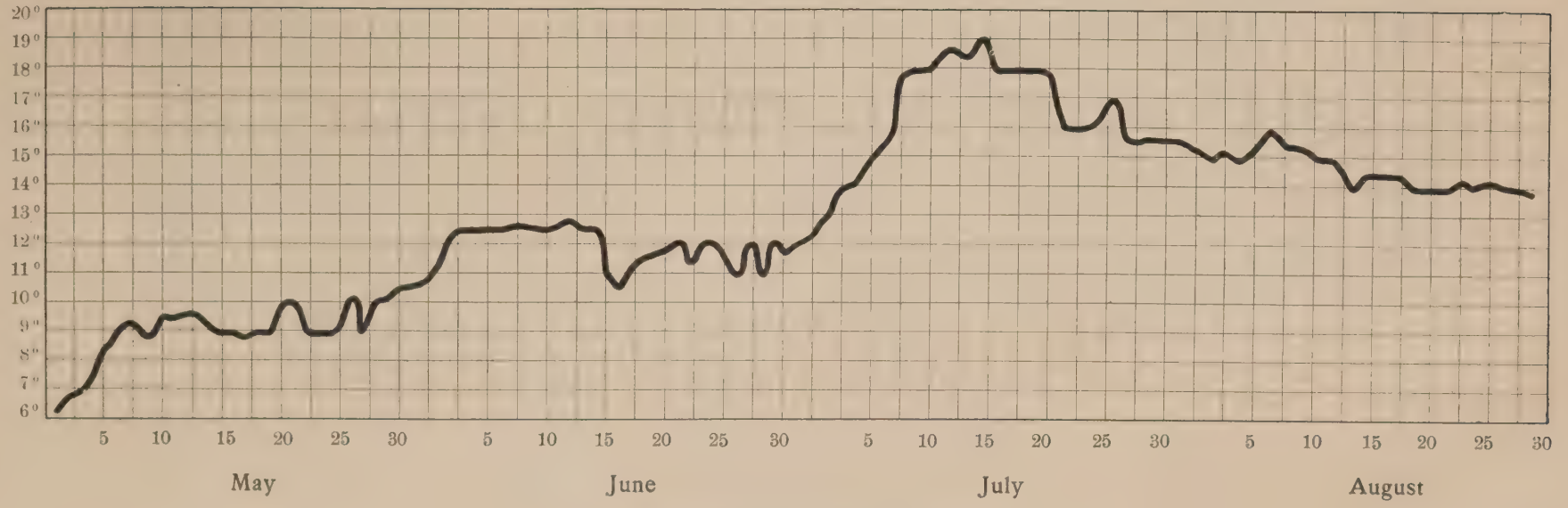

Fig. 4. Surface temperature at 8 a. m. at Oddesund.

The investigation has been carried out in the following way. The oysters in question have been opened, one or more pieces of the reproductive organ cut out, and the contents pressed out on an object-plate and then examined under microscope. By this method certain types have soon been identified within the sample at hand, and pieces of the generative Organ from representatives of these types have then been fixed in formaline sublimate for the purpose of later melting down and examining in sections. It ought to be added that notes concerning the contents of the intestine of the oyster, the state of the crystalline style etc. have been taken down, and that, so to say, all the examined specimens have been measured. Besides these 1400 oysters, which have been more thoroughly investigated, I have had an opportunity of making a still larger number the object of macroscopical investigations. It is true, that through macroscopical investigations we cannot as a rule obtain any definite information concerning the state of the reproductive organ, it is however possible, especially through some training, to make observations which may, when applied with due caution, serve as a supplement to the results otherwise obtained.

Before entering on a description and discussion of the different stages of the generative organ, I shall say a few words about the breeding time of the oyster in the Limfjord, meaning by breeding time the period in which are found oysters with eggs in segmentation (the so-called "white-sick" oysters) or with larvæ (the so-called "blue-sick" oysters) between the shells. This question has formerly been treated by C. G. Joh. Petersen (1907 p. 51. and t. 1—3) who in 1895 found the duration of this period to be from June 14th to August 24th, in 1906 (his investigation now only comprising a single locality) from June 18th to August 8th. Collin (1871 p. 203) mentions an individual with spawn on September 28th. As to the oyster grounds of Sleswig, Möbius (1871) stated the length of the breeding period as from the beginning of June to the end of August. Helland-Hansen (1907 p. 78) mentions the Norwegian oyster basins (Poller), stating the breeding in the warm basins to be June-August. He further informs us that in the colder basins the oyster is not to be found with fry until August—September, sometimes even October in especially cold years. In exact agreement with the conditions in the Norwegian basins I have found the breeding time in the Limfjord to vary according to the temperature; in 1919 spawn was found in the oyster from $^{13}/_{8}-^{29}/_{8}$, in 1920 from $^{9}/_{6}-^{10}/_{8}$, whilst in 1921 white-sick oysters were found already on May 20th; finally in 1923 fry was only found after July 6th. It ought to be mentioned here, first that the investigation has comprised a few thousand individuals in all, further that oysters were also examined in the days directly before and after the above named dates for the breeding times, so that we may take it for granted that no oysters containing spawn were to be found in the Limfjord, at any rate not in a number worth mentioning, outside of the above named periods. If we turn to the temperature in the Limfjord during the years in question, we also meet with a perfect agreement here; Fig. 1 shows the curve of the surface

temperature of the water at Oddesund during the months of May–August 1919, Figs. 2, 3, and 4 the corresponding diagram for 1920, 1921 and 1923. We see that in 1919 the temperature was 7°—8° C at the beginning of May, during the following days till the 25th it gradually rose towards 15°, without however surpassing this degree; similar conditions prevailed in May of the following year, the temperature yet rising a little higher, whereas later in the summer the temperature was rather considerably higher than the year before. In 1921 the temperature was in May essentially higher than in the two preceding years, i. e. 12° at the beginning of the month, 15°—17° at the end of this and the beginning of the next month; later in the summer the temperature decreased and became as low as in 1919 and 1920 or even still lower. On the other hand, in 1923 the temperature was in May — June as a rule below 12°, on $^1/_7$ it began rising fast, reaching to 17,7° on $^{10}/_7$ and culminating at 19° on $^{17}/_7$, when it decreased abruptly. From all these statements it appears that there is a certain connection between the temperature and the breeding time, so that the warmer the spring, the earlier the breeding time occurs, and the colder the summer, the longer this breeding time lasts. This is, however, not to be interpreted as if the temperature only has to surpass a certain limit, and oysters with fry are to be found. In 1921 when the temperature was 10°—12° already at the beginning of May and had been especially high during all the spring, oysters with fry were found even at a temperature of 13°—14°. The two preceding years when the temperature only began rising in the middle of May, fry was not found in the oysters until the temperature had for several days been about 15°, and in 1923 no fry was found until a temperature of 16°—17° had been reached. Thus it will hardly be possible to put down definite limits for the temperature of the commencing of the breeding time, as this limit will be the higher, the more steeply the curve of the temperature rises. The above mentioned opinion, put forth by Orton (1920, p. 343) that oysters breed at a temperature of above 15°—16° and continue as long as the temperature is beyond this limit can, therefore, hardly be correct.

One more question naturally presents itself in this connection, i. e. the number of the oysters with fry in proportion to those without fry. In the literature we find some information concerning this subject; even Davaine (1853 p. 21) had given the number of males as 100 times that of the females; also C. G. Joh. Petersen (1907 p. 52) considers the number of oysters with fry to be scanty; finally Dantan (1913 p. 871) is of opinion that he has demonstrated the number of females to be increasing with age till it reaches a number of 25 % of the total sum of individuals. In contradistinction to these statements, Möbius thinks that the number of males and females is equal (1881 p. 6). Further information is given by Hoek (1884 p. 489) who found among 190 oysters from natural oyster grounds 31 with fry, 49 ♀, 100 ♂ and 10 with only slightly developed sex organ. Of 190 "cultivated" oysters which were taken at the same time (at the end of June) the corresponding numbers were 28, 32, 92 and 38. Thus the per-cent of oysters with fry

is c. 15 in both cases. As regards these statements, it ought to be emphasized that, except for those by Hoek, they are in no case based on any histological investigation of the sex organ. Finally we find also in Hagmeier (1916 p. 225) some enlightment of this subject; we have, however, here to do with some oysters which had been placed in a tank at List in Sild where the hydrographic conditions are different from those in the nature, the numbers, therefore, not being quite fit for a comparison with such as are based on investigations in the nature. Hagmeier found the percent of oysters with fry to be varying, as it was in June c. 10, at the beginning of July 15, and at the end of this month 2,5 %. As to the Norwegian basins Helland-Hansen (1907 p. 78) writes that the whole stock of oysters breed in the warm basins, whilst only a few individuals breed in the colder basins.

If we now look at the conditions of the oysters in the Limfjord, my investigations have served to prove that during the three years when I had an opportunity of studying these animals there were c. 14,5 % of the total stock of oysters with fry directly at the beginning of the breeding time, and that this number had gradually decreased to 1 % at its close. In 1919 from the beginning of breeding time till July 1st, 89 oysters, of which 13 with fry (14,6 %) were opened; in July 301 were opened, of which 24 with fry (7,8 %), and from August 1st till the close of the breeding time 433 oysters, of which 4 with fry (0,9 %). In the following years the numbers were almost the same; from the beginning of breeding time to the end of June 392 oysters were opened, 57 with fry (14,3 %), in July (investigation especially going on in the latter half of this month) 222 were opened, 4 of which with fry (1,8 %), and from August 1st to the close of breeding time 211, 4 of which with fry (1,9 %). In 1921 it was only a rather small number of oysters which were opened after the beginning of breeding time, the numbers however still point in the same direction; from the beginning of breeding time till the end of May 22 oysters were opened, 2 of which with fry, in the first days of June 23 oysters, 3 of which with fry. Later in the summer only few oysters were investigated (some samples from different localities each of c. 20 specimens); only a single one was found to have fry, so that the per-cent most likely was small. If we now look at the different localities we get the same impression, f. inst. at Trehuse Hage in Sallingsund 64 oysters were taken, $^{20}/_{6}$ 1919, 9 of which with fry; 49 oysters, $^{23}/_{7}$, 6 with fry, and $^{26}/_{8}$ 47 oysters, none of which with fry. At the same locality were taken, $^{9}/_{6}$ of the following year, 30 oysters, 2 of which with fry, $^{23}/_{6}$ 20 oysters, 2 with fry, $^{16}/_{8}$ 20 oysters, none with fry. At Mullerne in Nissum Broad 100 oysters were taken $^{25}/_{6}$, 7 of which with fry; $^{31}/_{7}$ 75 oysters, none with fry, and $^{10}/_{8}$ 89 oysters, 2 of which with fry. The numbers from the other localities are in good agreement with these, 10—15 % of the total stock of oysters have fry at the beginning of the breeding time, then the per-cent gradually decreases in the course of the summer. Thus we see that the greatest per-cent of individuals with fry is met with at the beginning and not, as might perhaps be expected, in the middle of the breeding time, and what is still more astonishing, an increase in the tem-

perature of short duration later in the summer does not seem to be of any consequence to the number of breeding oysters. In the latter half of July 1919 the temperature in the Limfjord was considerably higher than in June of the same year, which did not, apparently, cause any increase in the number of oysters with fry. Also in 1920 the temperature was higher in a great part of July than in the last part of June, but likewise without any effect to the above named number.

From the above I mean to be allowed to draw the following conclusions, first that oysters with fry in their mantle cave may occur at a temperature about 13°—15° C, the more gradually the temperature has been rising in the course of spring the lower the temperature at which they occur (this will in the Limfjord generally be in the first days of June), further that the number of oysters with fry will directly after these days be a little less than 15 % of the whole stock, and finally that, in case the temperature does not rise considerably in the nearest time, this number will decrease in the course of the summer, so as to be c. 1 % at about the middle of August, after which time the breeding must practically be said to have come to a close. There will, however, after this date, especially in cold summers, now and then be found a few individuals with fry as f. inst. the above named case, mentioned by Collin.

After these introductory remarks I shall now pass on to a more thorough discussion of the different stages of development of the generative organ of the oyster, and naturally begin with the quite young oysters. I must, however, call attention to the fact that in the years when I was investigating the oysters in the Limfjord, the spat of each year was rather scanty; this was also the case in the directly preceding years, so that the material at my disposal of quite young oysters, i. e. of 1—2 years, has been small.

As already mentioned in the first chapter, the question how early an oyster begins spawning has been made an object of discussion in the literature, the different authors however highly diverging in their view on this subject. Davaine states (1853 p. 27) that he found oysters in September with a shell diameter of below 2 cm, and which were yet containing movable spermatozoa with distinct flagella. Davaine thinks, on the other hand, that eggs are only developed in oysters of considerable size and age, in which opinion he was confirmed by oyster sellers in Le Havre. Also Van Beneden (1855 p. 253) has come to the result that oysters only commence producing eggs at the age of 3—4 years. Contrary to this, Gerbe maintains that already among 1 year old oysters we may met with a considerable number with fry. Of 435 oysters of an average size of 2,5 cm in diameter, which could with certainty be stated to be 1 year old, he found 35 with fry, 127 with ripe eggs, and 189 with ripe spermatozoa. Based on experiments made in Roscoff, Lacaze-Duthiers (1893 p. XXVII) has come to the conclusion that a very small number of oysters produce fry in the first years, but that the main part of a stock only start producing fry in their fourth year. This is again contradicted by Dantan (1913 p. 871) who communicates that of 133 oysters,

1 year old, 9 had fry. Finally Orton (1921 p. 600) states having found an oyster which was beyond any doubt belonging to the fry of that summer and which had ripe spermatozoa in the very next autumn, i. e. a case corresponding to the one mentioned above by Davaine. Orton combines this case with the high temperature in the summer 1921. Later on Orton (1922 p. 213) has pointed out that in 1922 there were spawning females at Plymouth among the largest of the oysters born in 1921. Thus it is a matter of fact that oysters can produce ripe spermatozoa even in the very summer in which they were born; whereas the question whether an oyster be egg producing in its second summer or only in its third or fourth is a source of disagreement between the different authors. But if we look at the localities from which their material originates, it turns out that Dantan and Gerbe have had theirs from Arcachon, whilst Lacaze-Duthiers, Davaine and Van Beneden had theirs from the Channel and the North Sea, that is from localities with a much lower temperature than Arcachon. This might indicate that the date, at which an oyster for the first time starts producing eggs, varies according to the temperature and consequently occurs at an essentially earlier date at a warm temperature than at a colder one. Therefore we cannot say that an oyster starts producing fry at any definite age-limit. If we now turn to the conditions in the Limfjord they seem to support this opinion. The smallest oyster with fry, found by me, measured 6,5 cm from umbo to the opposite shell border and must, therefore, have been at least 2, possibly 3 years old as it had been taken in Livø Broad. The question how old an oyster is can as a rule only be determined by estimation as the growth rate is rather highly dependent on the salinity, wherefore the size and number of the growth rings are not to be used as absolute criterions. From oysters having attached themselves to objects which have lain in the water a definite time we have, however, gained some experience as to the growth and size which they may acquire in the course of a certain time, so that we are able to judge with some sort of certainty of the age of the individual in question, by aid of the length from the umbo to the shell border combined with the thickness of the shells, and with proper allowance for the locality. In late summer the lamellæ added to the shells in the course of the summer are often easily distinguishable as they are still quite thin and light. The question of the growth of the oyster in the Limfjord has besides been thoroughly treated by C. G. Joh. Petersen (1907 & 1908) I shall therefore not enter on it in details here. All the other oysters with fry which I have taken in the Limfjord were in Livø Broad above 7 cm, the majority 8 cm or more; in Nissum Broad I never found oysters with fry of less than 10 cm. The considerable size, which the oyster here obtains at an earlier date than usual, is, as above mentioned, first of all connected with the higher degree of salinity, but may perhaps also be due to the temperature being lower out here further West than in the inner Broads, for which reason the oyster in Nissum Broad should only commence spawning when 3—4 years old, whilst in the inner Broads it might start when 2—3 years old. The age at which the oyster com-

mences spawning is, however, no more alike in every single locality than in the various parts of its range of distribution, as the different individuals seem to disagree in this respect. I shall further discuss this matter later on.

The material of the O-group — i. e. oysters born during the spawning season directly previous to the investigation — which I have had an opportunity of observing, was as above mentioned rather small, only 10 individuals in all; none of these 10 individual however had ripe spermatozoa. I am, therefore, inclined to think that it will be correct to say that the oyster in the Limfjord does not as a rule produce ripe spermatozoa or, as already appears from the above, eggs, in the summer in which the individual in question was born. On the other hand, there is every reason to suppose, partly on account of statements in the literature, partly according to our conception of the function of the sex organ of the oyster (to which I shall come back later) that this theory does not hold good in very warm summers, when oysters of the O-group with spermatoza may be met with; theoretically there will probably be nothing to prevent us from finding individuals under optimum conditions producing eggs even in their very first summer. The three summers when I had an opportunity of making these investigations were however anything but remarkable for their heat. The temperature in the Limfjord was in none of these three years or in any of the following approximately as high as f. inst. in the summer 1914, the last of the great oysteryears.

The smallest oyster I have investigated measured from the umbo to the opposite shell border 1,6 cm; it was taken on $^{25}/_{7}$ 19 off Ejerslev in Livø Broad, i. e. in a place of no great salinity and consequently where the growth of the oyster is not especially rapid. Hagmeier (1916 p. 233) declares oysters having attached themselves to objects which have been 48 days in the water to be 1,9 cm in size; considering that the salinity at the west coast of Sleswig is a little higher, the above named individual must be supposed to be 40—50 days old and thus to have been born at the beginning of June; in support of this estimate, concerning the age of the oyster, it may further be stated that the shell of the individual in question was as thin as paper. If we look at the sex organ in this specimen it appears in sections as a distinctly visible anlage close below the outer epithelium outside of the liver. Hoek has in his work from 1883, frequently quoted before, given a description of the generative organ and its position in the oyster, I shall not, therefore, enter on a thorough discussion of the anatomical facts, in this paper. As shown by Hoek the reproductive organ of the oyster is placed between the hepatopancreas and the outer epithelium, in so far as it completely surrounds the first named organ and continues down into the so-called oral papilla where the excretory ducts are, and further in between the hepatopancreas and the pericardial cavity. The organ itself is described by Hoek as a net work of numerous anastomosing follicles and canals forming, as said above, a layer under the epithelium on the greater part of the animal. Outside of this "layer" of follicles the excretory organ is found in one part of the oyster.

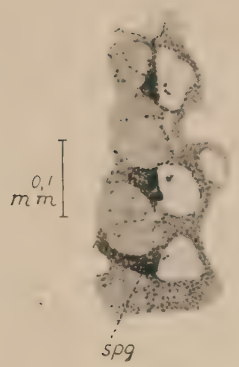

Fig. 5.

Commencing development of spermatozoa, in March, in an oyster of about 8 months.
Spg. Spermatogonia. × 100.

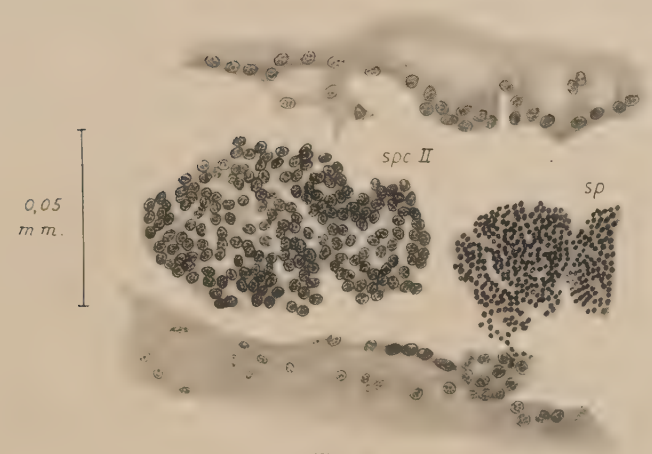

Fig. 6.

Advanced stage of development of spermatozoa in an oyster of 1 year.
spc. II. Spermatocytes II. Order. sp. Spermatozoa.

Figs. 5–10 Bodil Strubberg del. × 500.

Whilst the size of the hepatopancreas, as compared to the rest of the organs, especially the sex organ, is not particularly great in older oysters, it is otherwise in quite young oysters. Here the hepatopancreas and, on the whole, the intestine is relatively much larger in size, as they almost totally occupy the body of the animal, so that there is only an exceedingly thin layer of connective tissue between these organs and the epidermis. In this layer we may in the above mentioned individual of 50 days observe partly a line of small cells with large chromatinous nuclea, partly sometimes in this line very small, rather crescent-shaped cavities, the convex wall of which, turning towards the surface of the animal, is covered by a single layer of cells, whilst the inwards turning concave wall is strongly thickened and consists of a considerable number of small cells with large nuclea. These nuclea are strongly chromatinous, and, after colouring with hæmatoxyline, a little more than a dozen small grains may be detected in the nuclea; on the other hand, no mitoses could be observed in the individual at hand. From a comparison with a little older individuals and with the appearance and position of the sex organ in these latter, it will be clear that the above named cavities and the tissue of cells must be considered as the first anlage of the follicles of the reproductive organ and as the mother cells of the sex cells. There is no possibility for distinguishing any differentiation of sex at this stage. The other oysters belonging to the spat of this same year, which I had an opportunity of studying, were all somewhat older; they were about 2,2 cm in size, and as the individuals in question were all taken at the end of August (in Livø Broad) they must be supposed to be c. $2^1/_2$ months of age. In these specimens quite a similar anlage of a sex organ was found which seems, therefore, to be the stage to which the sex organ will reach in the first summer, at any rate under the conditions usually predominating in the Limfjord.

If we now observe an oyster in the spring following the summer in which it was born, we will find the above named anlage further developed. In the month of March I have in quite small oysters, 2—3 cm in size, found the above mentioned cavities to be rather much widened, whilst the number of small cells in the inside walls of these cavities had simultaneously considerably increased. Sometimes these cells were lying freely in the lumen of the cavities, forming small heaps, and the whole image was strongly recalling the spermatogenesis (Fig. 5). Already in the month of May I have in oysters with a shell diameter of a little above 3 cm found fully developed spermatozoa with flagella, gathered in the heaps characteristic to the oysters. Also sections of such oysters clearly demonstrated the spermatozoa to be present, but besides the heaps of spermatozoa I always found in the above named follicles several of the before mentioned mother cells of spermatozoa, so that it seems as if a spermatogenesis is constantly taking place at this stage. (Fig. 6). The spermatogenesis apparently is continued for some time in the summer; several sections of small oysters, 3—4 cm large, from the month of June lend a very fine image of the mentioned follicles with one or more heaps of spermatozoa in the middle, surrounded by spermatozoa mother cells. In sections from such

oysters from the month of July the generative organ is seen to be completely filled with heaps of spermatozoa. This seems to prove that the oyster in its second summer under the usually predominating conditions in the Limfjord produces ripe spermatozoa and thus functions as a male.

As far as the older oysters are concerned, an investigation of their sex organ leads to rather strange results, as it already appears from the works of previous authors, especially that of Hoek (1883 p. 219). Hoek distinguishes between 5 stages or types of the development of the reproductive organ of the oyster. Partly such in which the generative organ so to say exclusively contains ripe spermatozoa, partly such in which it is filled with eggs; these latter he once more divides into two groups, i. e. those with a number of spermatozoa not worth mentioning, and those with ripe spermatozoa in the genital ducts. Finally the fourth and fifth types are those having unripe eggs in the follicles, besides spermatozoa and spermatogenesis and those containing a few eggs and besides spermatogenesis. These latter have often spawned a few weeks before the investigation and are, according to Hoek, females having now passed on to the male stage, whilst the last type but one of the 5 types consists of males which are passing on to the female stage. Hoek's investigations only took place in the summer, and he says himself that he had but a scanty number of oysters at his disposal. For these reasons Hoek does not, as already mentioned in the summary of literature, thoroughly discuss the question of the consecutive order of these stages, nor of the factors influencing and regulating it. He seems to be of opinion that the oysters which function in one summer as females become males in the following summer, and vice versa, and that about half a stock thus produces alternately eggs and spermatozoa every second summer, while the other half produces the opposite.

Having thus recorded the results obtained by Hoek, I shall now pass on to an account of the observations made by me during my investigations of the reproductive organ of the oyster in the Limfjord. As said above, this question has not till now been the object of a discussion, and since the publication of Hoek's paper the generative organ of the oyster has been left so to say unstudied. If a not too small number of oysters in the Limfjord are investigated during the spawning period, one cannot help being struck by the majority of the oysters at the male stage compared with those at the female stage, as was the case in my years of researches there. Davaine and Hoek have already made this observation, as said before, and several authors have mentioned the small number of oysters with spawn which is usually found when a stock is investigated; that it was so in the Limfjord, at any rate in the later years, has likewise been stated by me in the above.

In order to give an idea of the numbers in the Limfjord I shall state as follows: Of 64 oysters, dredged at Trehuse in Sallingsund $^{19}/_{4}$ 1919, 44 were males, of 50, dredged $^{4}/_{7}$ in the same year off Kaas, 40 were males, of 37, dredged $^{17}/_{7}$ in the same year and in the same locality, 30 were males, of 47 oysters, taken by

diver in Nissum Broad $^{21}/_{7}$ 1919, 44 were males, of 50, taken at Kaas $^{22}/_{7}$, 31 were males, of 48, taken at Ejerslev $^{25}/_{7}$, 40 were males, and finally of 49, dredged at Trehuse $^{26}/_{7}$, 33 were males. By males are in every case meant individuals containing considerable numbers of spermatozoa with distinct flagella. In contradistinction to this, the number of females in the above mentioned cases was extremely small. Of the 64 above named only 2 were females, of the 50 from $^{4}/_{7}$ 5 were females, of the 37 from $^{17}/_{7}$ 3 were females, of the 47 from $^{21}/_{7}$ only 2 females, of the 50 from $^{22}/_{7}$ 6 females, of the 48 from $^{25}/_{7}$ only 1 was a female, and finally of the last 49 8 were females. The remainder of the individuals were in the above mentioned cases either oysters with spawn, that is, individuals having been females, or different transitory stages between the two sexes.

These numbers are only examples. On all occasions when I opened oysters within the above named dates I have met with similar numbers, also in the following years. By these researches we thus come to the result that in the years since 1919 there were in no summer and at no time in the Limfjord more than about 8—10 % of females, i. e. oysters containing in their reproductive organs exclusively, or so to say exclusively, large eggs, completely filling and expanding the follicles. Opposite to this, we have about 75—80 % of individuals producing spermatozoa.

After thus having stated the first main impression which presents itself when a stock of oysters is investigated for the purpose of comparing the numbers of males and females respectively, I shall now pass on to a more detailed study of these numbers. If the stock is not examined collectively, but is divided into classes of various sizes, it will be seen that the proportions are somewhat different. Among the above named samples from the summer 1919, comprising 345 individuals in all, the main part was, as said above, males (262), whilst only a small part (27 in all) were females. If we leave out, however, all individuals of less than 7 cm, i. e. all the oysters from the years 1917 and 1918, it appears that among these (44 in all) there is no female. Thus individuals at the female stage are to be found principally among the older oysters. This is also in good agreement with the fact, stated by me in the above, that oysters with spawn are only met with among individuals which are at least two years, usually three years old. It has already been mentioned that oysters in the Limfjord do not, at any rate not as a rule, produce spermatozoa in the first summer, in the second only spermatozoa. If we proceed to the third summer we see that the above named sample likewise contained no female, and it must be stated that oysters producing ripe eggs before the fourth summer, i. e. the summer in which they are 3 years old, are at least not generally to be found in the Limfjord.

This is not, however, without exceptions, as I have found a few oysters having eggs already in their second or third summer. The smallest oysters with egg- filled follicles, seen by me, were between 4 and 5 cm in size. They were found at quite low water, the depth being only a little above $^{1}/_{2}$ m, at the

entrance to the afterwards embanked lagoon Klovvig at the north point of Venø. On the gravel bottom of this entrance a great number of small oysters of about equal size and consequently probably of equal age were found. Their size was, as said above, about 4—5 cm. They were taken $^{19}/_{8}$ 19, and it was very easy to see how much these oysters had grown in the summer 1919, as the part of the shell which had been formed the last was by its lighter colour clearly distinguished from the part having been formed during the previous growth period. They had grown 0,5—1,4 cm in the course of the summer, so that at the end of the summer 1918 they cannot have been more than 3 cm, which is the size generally obtained by oysters in the autumn following the summer in which they have attached themselves. We had, therefore, to do, no doubt, with oysters of the year 1918, and they were now at the end of their second summer. The eggs were almost quite ripe, with a nucleus similar to that of the eggs of an oyster which is going to spawn, so that it is to be supposed that these oysters would be able to spawn, at any rate in the following, i. e. in their third summer. These are the only oysters of 1 year which I have seen with eggs, and they were, as mentioned above, taken in very low water and towards the end of the spawning period. As said before, I have found a single oyster, possibly only two years old, which had spawn, and I have also found some few individuals of two years with eggs. That makes, however, only 4—5 individuals in all, so that under the conditions of temperature predominating since 1914 it must certainly be stated to be the normal occurrence that the oyster in the Limfjord does not produce eggs until it is three years old.

We may then for the present, on account of these observations, take it for granted that since 1919 (probably since 1914) there has not been any year in which oysters in the Limfjord have started spermatogenesis in the summer in which they were born; that in these years it was only exceptionally (at low water) that oysters of 1 year contained eggs, whereas individuals of one year have normally been producing spermatozoa; that a few individuals have had eggs in their third summer, the main part however not until the fourth summer i. e. when they are three years old, and finally that even among older oysters there are only few individuals at female stages (c. 10 %) whilst the chief part (c. 75 %) are males; the relatively only small number of spawn-producing oysters is consequently due to the small number of females.

Besides the males proper with a reproductive organ containing spermatozoa exclusively and the females proper with follicles containing eggs exclusively, or so to say exclusively, we further find, when investigating a stock of oysters in the spawning period, a certain number of other stages, which were sometime by Hoek regarded as transitory stages between the two sexes. That a change from male to female and vice versa is taking place in one and the same individual has already been stated by Davaine, as above mentioned, and Möbius and Hoek have likewise demonstrated that individuals, which have produced spawn, are later in the summer containing spermatozoa in their generative organs. That a change from

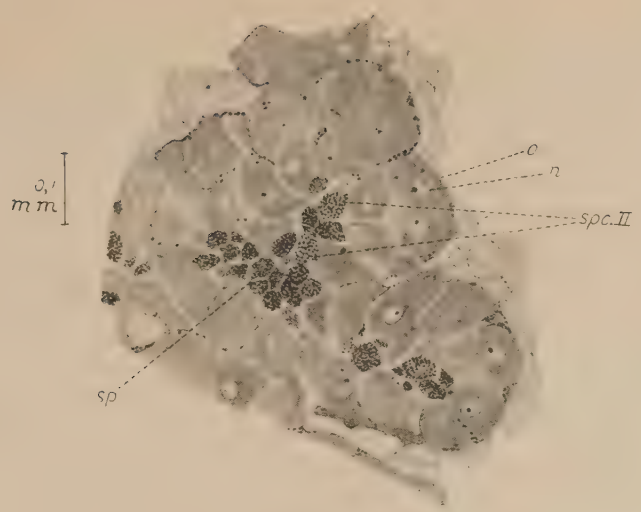

Fig. 7.

Section of oyster still producing spermatozoa, but with advanced egg-development. June.
o Egg, n Nucleus, spc. Spermatocytes II Order, sp. Spermatozoa. $\times$ 100.

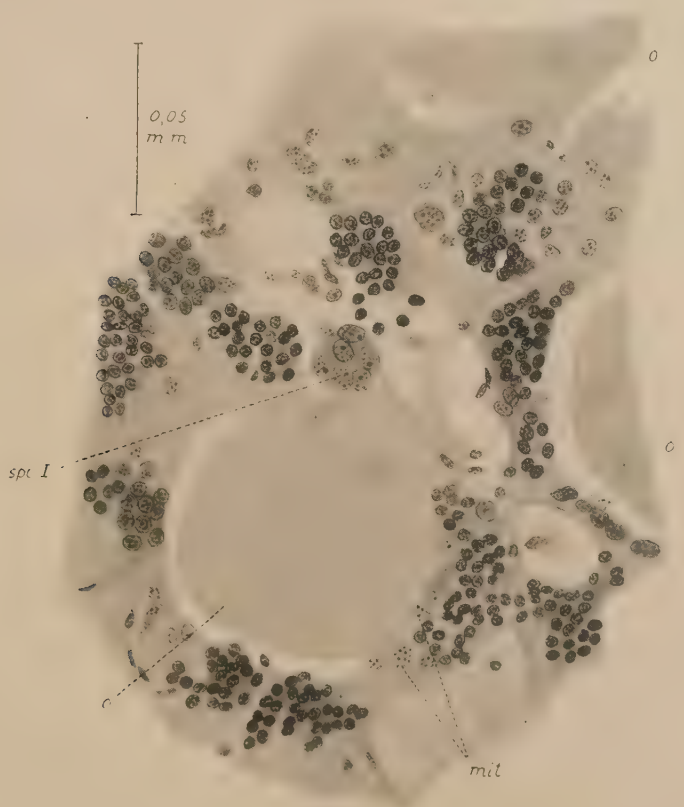

Fig. 8.

Section of oyster having started spawning, with commencing development of spermatozoa. July.
mit. mitoses. $\times$ 500.

female to male is going on is a fact which has been observed by so many authors that there can be no doubt as to its correctness. Besides the above named earlier authors Orton (1921 P. 586, 1922 P. 212) has quite recently, with reference to this change, made several interesting observations and experiments, by which it has been confirmed partly that this change is really taking place, partly that the change from female to male is made very quickly, as an oyster having spawn $^{3}/_{7}$ produced ripe spermatozoa already $^{18}/_{7}$. Whether an oyster has spawn is easily stated — without killing the animal — as a little spawn will always be flowing out between the shells, but it is connected with greater difficulties to state whether an oyster produces spermatozoa, unless the shell be opened, whereby continued observation of an eventual sex change in this individual is prevented. When Davaine and Hoek came to the conclusion that a change from male to female also took place, they could not support this idea on direct observations but only on the occurrence of certain spermatozoa producing individuals, in the sex organ of which a beginning egg-development could besides be seen, and which were, therefore, supposed to be transitory stages between male and female. In order to have it definitely proved that these stages really are such transitory stages and that a change, not only from female to male but also from male to female, is indeed taking place, I made, in the summer 1919, some attempts of boring a hole in the shell of some oysters as a means of determining the sex without killing the animals. This was very easily done; with a common borer a hole of c. 5 mm in diameter was made in the flat shell, a pipette was then through this hole inserted into the reproductive organ of the animal, and a sample of the genital products in this way procured. Apparently the animals did not suffer any damage worth mentioning through this treatment, the hole in the shell was very soon shut by a thin lamella which was, however, easily pierced by the pipette at the next investigation. The examined individuals were either placed in aquaria or in the oyster tanks at Ørodde at the Limfjord. Through this method I succeeded in observing first several instances of the change from female to male, in further confirmation of the correctness of this fact, but besides also some instances of the change from male to female. An individual which was a male $^{6}/_{6}$ 19, was a female $^{15}/_{7}$, even $^{8}/_{7}$ it had ripe spermatozoa in the characteristic heaps. Another individual with ripe spermatozoa $^{20}/_{6}$ had distinctly eggs $^{4}/_{7}$, these eggs were in segmentation $^{20}/_{7}$, and $^{25-26}/_{7}$ the pelagic fry was swimming out. Still another individual, distinctly a male $^{20}/_{6}$, contained spermatozoa even $^{4}/_{7}$, but visible eggs $^{15}/_{7}$. I have a few more instances of such a change at hand, so that it may now be considered a fact that this change really takes place and that the above mentioned supposed transitory stages belong to individuals which are passing from the male to the female stage. Whilst the transition from female to male is, according to observations by previous authors as well as the experiments by Orton, very rapidly performed — with which I fully agree — so that no transitory stage proper can be stated, the transition from male to female proceeds more slowly, and all gradations from a faint

egg-development to follicles almost filled with eggs and with minimal spermatogenesis may be found. Only when the eggs are fully ripe and almost completely filling the follicles the spermatogenesis ceases, in several cases some spermatogenesis may nevertheless be stated in a few follicles, but these sperm-filled parts are always minimal, compared with the egg-developing parts. A very sharp limit between the transitory stages between male and female on one side and the female stages proper on the other is, therefore, not to be stated in all cases. A great number of individuals which seem at a preliminary examination to be males proper will likewise at further investigation turn out to be at a transitory stage with a beginning egg-development. If the sex is determined by means of pressing out some of the contents of the generative organ on an object-plate and then observing them under microscope, the eggs will only be visible in case the egg-development is rather advanced, otherwise only the fully developed genital products, the spermatozoa, are detected. In several cases I have, by means of sections, stated a more or less advanced egg-development in individuals which had through such a preliminary examination been determined to be males proper (Fig. 7). As however the main part of my determinations of the sex has not been performed by means of sections but in the fashion described above, I may be justified in supposing that among the above-mentioned many males, amounting to 75 % of the stock, there were some which had in reality begun changing into females, although the eggs were still quite small. Thus the limit between the males proper and the transitory stages from male to female is not quite sharp either. It ought, however, to be remarked that a long time after the egg-development has set in, the animal constantly functions as a male, producing ripe spermatozoa, so that we would be justified in indicating these individuals as males, which is what I have done. In the above-mentioned experiments, at which a transition from male to female was observed, this transition was apparently quickly performed, as eggs were found 8 days after the reproductive organ had been filled with spermatozoa. This case is, however, identical with the case above; it is true that these individuals have functioned as males till shortly before starting their function as females, but we may take it for granted that while apparently males proper they have had a rather advanced egg-development. In these individuals the generative organ could only be examined by means of removing some of the contents by a pipette, and it was, therefore, only some of the spermatozoa which were caught as they were still present in a greater majority than the unripe eggs. As said above, I have in several instances stated this to be the case as I have killed the animal, examined the sex organ in sections and by this proceeding proved that, even when the eggs were rather large, only spermatozoa could be pressed out of the reproductive organ. Thus the transition from male to female is a very smooth and slowly proceeding process.

In the above it has been mentioned that the transition from female to male is more quickly performed. Already Davaine had observed that oysters with larvæ

in their mantle cavity (blue-sick oysters) produced spermatozoa, and Hoek and Orton have also demonstrated that the transition takes place directly after spawning. I have had the opportunity of examining some oysters which had just begun spawning in the very moment when they were opened; one of them had spawned some of the eggs; some eggs had flown out and lay in the tank as a white cercle surrounding the animal. The newly spawned eggs were most often segmentated or became so after the lapse of some time, so that they must have been fertilized either in the generative organ or in the genital ducts. That this is a fact has been observed before by Waalewijn (1882 P. C. I.), who was even fortunate enough to see the eggs in segmentation pouring out through the genital aperture. It is, however, not always that the eggs are spawned in segmentation, as I have in a single case found unsegmentated eggs in the mantle cave; after having been left in a dish for some hours segmentation began. In the cases when only a small part of the eggs had been spawned, and when the sex organ was still amply filled with eggs, spermatogenesis was undoubtedly in certain places setting in. In the follicles, from which the eggs had been discharged, there was a very active celldivision going on with mitoses in the thickened inner part of the follicles, even in the follicles which were still filled with eggs, there were places where spots consisting of many closely gathered small cells with strongly coloured nuclea, undoubtedly spermatogonia, could be detected. In individuals having spawned the larger part of the eggs this spermatogenesis was much more advanced (Fig. 8). Distinct heaps of spermatocytes were to be seen all about, sometimes lying freely in the follicles. In the cases when all the eggs have been spawned (i. e. in white-sick oysters) the above named heaps of spermatocytes are to be seen in the follicles, now all lying freely. It is, however noticeable that the spermatogenesis setting in directly after the spawning process, is very scanty; only very few heaps of spermatocytes are found in each follicle, and in oysters having recently been females, we never meet with the considerable spermatogenesis with completely filled follicles which may be observed in the later period of the male stage. The period during which the oyster is white-sick being of rather short duration (3—4 days), which will be further discussed in the following, we meet with an advanced spermatogenesis with freely lying heaps of spermatocytes in the same follicles which were filled with eggs, 4—5 days before. It is, therefore, easily comprehensible that ripe spermatozoa may be demonstrated in these individuals a few days later, which has, as said above, been done by several investigators. Also I have had an opportunity of observing the change from female to male, through the above described experiments with oysters with pierced shell, and am therefore able to add supplementary remarks to the explanation above. An individual which was white-sick $^{17}/_{6}$ 19, was blue-sick $^{22}/_{6}$, and functioning as a male $^{8}/_{7}$. That this was really the case I have further made sure by fixing the individual in question and examining the sex organ in sections, whereby it turned out that the spermatogenesis explained above was here so far advanced that there were now spermatozoa between the heaps of spermatocytes

(Fig. 9). It is, therefore, entirely excluded that the ripe spermatozoa, observed in this oyster so shortly after it has functioned as a female, can have been introduced from the outside by the water, the section proves that they have originated in the sex organ of the animal itself. Sections of blue-sick oysters have besides served to demonstrate that even at the stage when the animal still has its larvæ in its mantle cave, the spermatogenesis is, as a rule, so advanced that ripe spermatozoa are present. The period, during which the oyster is blue-sick, is of varying duration, but rarely exceeds 5—6 days, so that we may say that the appearance of ripe spermatozoa sets in at the latest 10 days after the eggs have been discharged.

The result of an investigation of the stock of oysters in the Limfjord during the spawning period thus may be described like this: individuals at the male stage, i. e. individuals with spermatozoa, are in considerable majority, and they include almost all oysters of one or two years; among these individuals with spermatogenesis we meet, however, with a certain number with beginning egg-development, and some others which have been females and are characterized by their follicles being almost empty. In the two facts that the egg-development is a slow process, taking place while the animal is constantly producing spermatozoa, and that the spermatogenesis sets in almost immediately after the eggs have been spawned, we have a plausible explanation of the great majority of the male stages. If we reckon with this that spermatozoa may be produced until 8—10 days before the eggs are discharged, and that sperm is reproduced 8—10 days after the spawning process, as demonstrated through experiments and observations, we come to the result that the female stage proper, the stage at which so to say nothing but eggs are present, some time only lasts for three weeks at the most. In opposition to this, the male period in the Limfjord may last 2—4 years. As the duration of these two periods is so pronouncedly different, it is no wonder that the proportion in number between the two stages must turn out to be as stated above. That spawning oysters have been so very rare in the Limfjord in later years, and pelagic fry consequently scanty, must be due to the small number of females, which is again caused by the long duration of the male period. The transition between female and male being quick, and the transitory stages between male and female until the last stage appearing as male stages, it is likewise comprehensible that distinct transitory stages are also scanty; I have found about 10 % i. e. a number similar to that of the female stages proper.

We shall now pass on to discuss the oyster outside of the spawning period i. e. the time from the middle of August till about June 1. Within these dates I have examined oysters at different times, and it has turned out that in each of the months of the year we may meet with oysters at about the same stages as in the spawning period. The only difference is that the eggs of the females are not so large as during the spawning period, but individuals with the sex organ almost completely filled with eggs may still be found, although the nuclea of the eggs

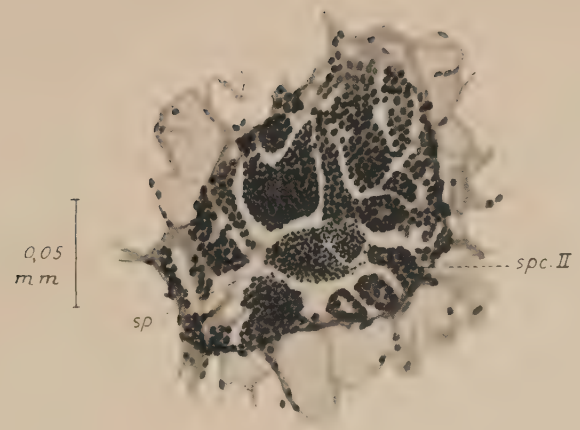

Fig. 9.

Section of the generative organ of the oyster, 3 weeks after Spawning. sp. II Spermatocytes II order. sp. Spermatozoa. × 300.

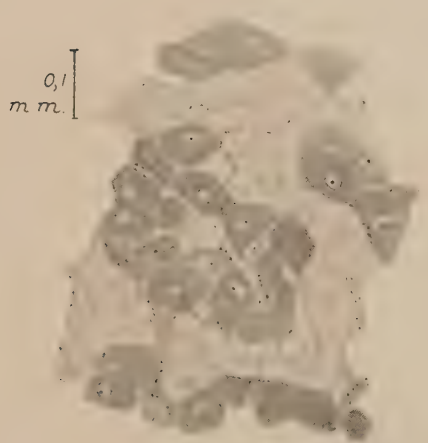

Fig. 10.

Section of the generative organ of a wintering female. November. × 100.

are somewhat differing in appearance from those of similar individuals in the spawning period. (Fig. 10.) Outside of the spawning period, the oysters completely filled with eggs have nuclea, in appearance similar to those observed during the spawning period in oysters in transitory stages from male to female. The female stages observed in autumn and winter must, therefore, be supposed to originate from individuals which have in the course of the summer completed the transition from male to female, but not had the time to spawn before the temperature began decreasing in autumn.[1]) Thus it is from these individuals that the first fry originates in spring. At the beginning of this paper I have mentioned the peculiarity that the % of spawning oysters is the greater in the first part of the spawning period; this must certainly be due to the facts that the sex change only takes place in the course of the summer and that a great number of individuals have time for egg-development but not for spawning, wherefore this process is put out till the following spring when the spawning period sets in. They are then spawning together with a certain number of individuals which did not proceed quite as far in the sex change in the course of the last summer, but which have, in the spring when the temperature is again increasing, overtaken these wintering females; this is then the explanation of the majority in spawning oysters at this very time of the year. Thus in individuals, which become females at the end of the summer, the female stage is of considerably longer duration than in the oysters becoming females at the beginning or in the middle of the summer, as in the latter it only may be of a duration of 3 weeks, whilst in the wintering females it is of about 6 months. Oysters which spawn later in the spawning period are those which did only get time for an insignificant egg-development in the previous summer. It must, therefore, be taken for granted that the development of sex cells and the processes of sex change practically cease in the autumn, and that the individuals remain and winter at the stage obtained till then. Just as certain individuals are wintering with their follicles filled with eggs we meet with others with follicles filled with spermatozoa in the winter, and, as said above, the different transitory stages also occur. Further in autumn and winter we meet with individuals with almost empty follicles or, at any rate, with only very slight spermatogenesis; these must be individuals having spawned towards the end of the summer. As mentioned above, spermatozoa are produced, directly after the spawning of the eggs, but only in relatively small numbers, and there is no sign that this sperm development is continued. This is most probably to be understood like this that the animals — after having within a short period produced spermatozoa, eggs and once more spermatozoa — live through a period of rest, and as far as the animals, having spawned later in the summer, are concerned, it is in the autumn that

[1]) It is these wintering oysters which are particularly enjoyed by oyster-eaters. The „feeding" of oysters in the cold Norwegian basins (Poller) consists in a checking through low temperatures of the egg-development, resulting in a great number of wintering females.

this period of rest sets in, wherefore these individuals will be wintering at this stage without sex-products[1]). It is possible, even most probable, that all the oysters which have produced spawn in the summer, winter at this stage. I must confess that I have not directly observed any transition to these stages of rest in any male having recently been a female, but different other circumstances indicate that these stages must have originated in this way. First of all this that the investigation of a certain number of individuals which have been found to be "blue-sick" seems to demonstrate that the spermatogenesis, taking place directly after the eggs have been discharged, is not continued, and that another stage with no formation of sex products must consequently follow. Further these „sexless" stages do not occur at the spawning stage proper but only in the autumn and the winter, the first of them were stated in the middle of August. In the course of spring, the spermatogenesis again sets in in these individuals which become males proper in the following summer, and possibly have egg-development already in this very summer; at a temperature like the one predominant in the Limfjord these later years, these oysters will, however, only in the following summer, at the earliest, be able to produce spawn, so that there must be at least two years between the spawn-producing stages of an oyster. That the above named individuals in the resting period cannot become females without an intermediate male stage is evident from the fact that a stage of spermatogenesis always precedes the egg-development. In the winter I have not investigated as large a number of oysters as in the summer time, and I cannot, therefore, speak with as much certainty of the proportion in numbers between the separate stages in the winter as in the summer. It has, however, struck me that the male stages proper do not seem to be by far so dominating in the winter as in the very spawning period. The reasons for this are rather obvious, the female stages are in the winter of much longer duration than in the summer, and the transitory stages do not appear so distinctly as male stages in the winter. As said above, the spermatogenesis is continued even after the egg-development has begun, so that the transitory stages will for a long time appear as male stages. In the winter there is no spermatogenesis, wherefore the transitory stages between male and female are not characterized by this spermato genesis. Finally it must be remembered that also the individuals which are found in the period of rest in the winter, have been males part of the preceding summer, so that, according to this, it is easily comprehensible that the female stages are more frequent in proportion to the male stages in the winter months, compared with the summer months. An investigation of a series of samples from January-February 1920, samples however not comprising more than c. 100 individuals in all, gave almost 50 % of female stages and transitory stages with advanced egg-de-

[1]) When Davaine, as mentioned above, means to have observed a recommencing egg-development to take place in an individual still having spawn in its mantle-cave, it is certainly due to a misinterpretation of some undeveloped eggs which are sometimes left in the follicles after spawning.

velopment. The development of sex cells has been practically interrupted from about September 1. till the beginning of April, as spermatogenesis and a continued egg-development are found in the course of April-May, and during this period the processes of sex change etc., interrupted since late in summer, are continued, resulting in the development of the stages which are described in the above to be found in the course of the spawning period.

The observations as yet put forth may be gathered in the following summary of the function of the sex organ of the common oyster under the natural conditions predominant in the Limfjord since 1914. In the year in which the oyster has attached itself, it does not produce any sex products, it is not until the following summer that this occurs, and it then produces spermatozoa, i. e. functions as a male. The egg-development may exceptionally be started already in the animal's second summer, and towards the end of the summer we may then find individuals with rather large eggs; this has however only been observed in oysters living in quite low water. Normally the egg-development only begins in the animal's third summer, and it even is an exception when it is terminated in the course of the third summer, ordinarily it, therefore, occurs in the fourth summer, that is when the animal is three years old. Consequently it must spend the third winter at the transitory stage between the first male stage and the first female stage. The normal proceeding will, therefore, be like this that the oyster discharges its eggs in the fourth summer. On this follows then a male stage of short duration with scanty spermatogenesis, after which it passes on to a resting period without formation of sex cells. At this stage it then passes the fourth winter, whereafter the oyster in the fifth summer once more functions as a male, in the sixth summer the egg-development recommences (if it has not already done so in the fifth summer), and in the seventh summer it functions a second time as a female, and so forth, till the animal dies. This is, as said above, a representation of the normal proceedings; in a few individuals the alternation seems to proceed more quickly, with shorter intervals between the female stages. Also in other localities of the range of the oyster, the proceeding is different; in waters with a higher temperature oysters are found, as mentioned above, to spawn a first time at any rate in the second summer, it is, therefore, to be supposed that the whole of the alternation proceeds more speedily.

According to this description, the common European oyster (*Ostrea edulis L.*) may thus be characterized as a protandric alternating hermaphrodite, as it starts as a male and then, in the course of its life, constantly alternates between stages of male and female. The idea of an alternation is, as often stated, not in itself new, as Davaine, the first author, who studied these facts more in detail, approached this thought, and later on Möbius and Hoek have also advocated a sex change to be present in the oyster. That the idea of this alternation was neither a success nor generally acknowledged is partly due to the fact that no attempt was made of bringing about an agreement between the theory of alternation and the different

stages found by investigation of a stock of oysters, and further, specially to this that nobody tried to find out in which way the different stages succeed each other, of how long a duration they are etc., so that a description of the function of the sex organ through all the life of a single individual might be given, according to this idea. It is such a description which I have tried to give in the above. Another circumstance, which has certainly contributed to make many authors unwilling to adopt the theory of such an alternation, is that the now rather frequent instances of sex change from different parts of the animal world had not then been stated. Through investigations of *Bonellia*, *Crepidula*, through those by R. Hertwig and his pupils of the hermaphrodite frog races, and through many other investigations we have experienced that, partly through the influence of outer conditions, several animal species are capable of sex change, of passing from females to males or vice versa. It is, therefore, nowadays not in advance so very incredible as it was 70 years ago that an animal may in the course of its life alternate between the stages of male and female. The fact that a zoologist with the position and authority of Lacaze-Duthiers was so decidedly in opposition to the theory of alternation has naturally also contributed to impede the acknowledgement of this idea.

In favour of the conception, stated by me in the above, are partly the direct observations of a sex change in both directions, partly the fact that the investigations, made at different times, of the sex organ of oysters agree with this conception. If such an alternation is not acknowledged, I do not see how it will be possible to explain the presence of the different transitory stages, and the alternation also yields, as mentioned above, an explanation of the peculiar proportion in number between the male stages and the female stages in the spawning period. Direct observation of the sex change from female to male has, as said above, not only been made by me, but partly by several of the first investigators, partly in the very latest time, after this investigation had been started, by Orton (1921 P. 586, 1923 P. 212)[1]). Orton's communications called forth some discussion during which some criticism and doubt as to the correctness of the alternation were uttered. Calderwood (1921 P. 273) partly expresses his doubt as to alternation in general, as he is of opinion that sex change only exceptionally occurs, partly emphasizes that it would have been of more importance if observations of a sex change from male to female had been made. This latter change has now been observed by me and, as to the first objection, it is true that it must be acknowledged that we cannot prove that all oysters have sex change. As it has, however, in the course of time been observed by 5—6 zoologists, both in France, Holland, Germany, England and Danmark, and in the last named countries even in a good many cases, I should think that we might, without being too bold, be justified in maintaining the alternation to be normal, and that each oyster, therefore, changes its sex

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[1]) Cp. post-scriptium pag. 84.

at certain intervals in its life. The investigation of the sex organ besides further confirms this theory.

The next question which arises now is: Which are the factors regulating this alternation? Two possibilities first present themselves, the alternation either proceeds regularly, in compliance with inner factors, independent of outer conditions, or is regulated by outer conditions, such as temperature, nourishment, salinity a. s. f. In the above the question of temperature has often been discussed, and much points to the temperature as a factor to which much attention is due. All facts connected with the alternation at any rate indicate that the duration of the different stages is not dependant on inner conditions, but are, on the contrary, highly dependant on the influence of outer conditions. As appears both from the literature and from my investigations, there is a great variation in the stages within the range of the oyster, and even inside of a few limited areas, such as the Limfjord. If we inspect the kind of this variation more closely, we see that it is always in agreement with the influence of the temperature.

According to Davaine as well as Orton, oysters in the Channel produce spermatozoa in their first summer, at any rate in warm summers. At the west coast of France it is rather common that they spawn before they are one year old, at the coast of England a few of the largest, one year old oysters, do the same (Orton 1922 P. 213), in the Limfjord oysters are exceptionally spawning when they are two years old, never before, and spermatozoa are not produced in the Limfjord until the second summer. The few individuals, which were stated in the Limfjord to have eggs already in the second summer, were found at low water, where the temperature of the summer is higher. Attention may further be called to the fact that, according to observations from the Norwegian spawning basins (Poller), the whole stock spawns in warm summers, not in cold, and that the spawning period is besides, in very cold years, put off even to the autumn (Helland-Hansen). Finally I have demonstrated on the first pages of this chapter that the colder it is, and the more steeply the temperature curve has been rising, the later the spawning period sets in. All these facts can only be interpreted like this that the temperature must be supposed to exercise a considerable influence on the development of the sex products, especially the eggs. The farther we go south the younger the oyster is, when it begins spawning, i. e. the shorter is the duration of the first male stage proper, and the more quickly the eggs are developed. For the same reasons it is comprehensible that the spawning begins earlier in warm years than in cold, and that the number of spawning oysters has been so small in the Limfjord, in the last years of low temperature. The rate of the egg-development depends on the temperature and increases with it; the higher the temperature, the quicker the egg-development, the shorter the duration of the transitory stages. The consequence of a higher summer temperature thus will be that the intervals between the spawning periods (the female stages proper) become shorter, so that each separate individual spawns several times in its life. According

to this, it might be supposed that at a high temperature there must be more females during the spawning period, as the transitory stages, appearing as male stages, would not be of so long duration, compared with the female stages, and consequently not so predominant in number as was the case during the later years in the Limfjord. Unfortunately, the only record concerning these conditions in the more southern waters, that we have at hand, consists in the numbers given by Gerbe (p. 20), and Dantan's statement that at Arcachon there is 25 % of females in a stock. If this number holds good for the whole of the spawning period, it is seen that it also highly exceeds the number found in the Limfjord, where it is only 15 % in the first part of the spawning period. As the female stage is of short duration, the occurrence of 25 % of females at a certain point of time does not mean that only 25 % are spawning. In case the spawning period be of long duration, there is nothing to prevent the whole stock from spawning, although there may be only 25 % at female stages at a certain moment. Even if we do not gain much information from Dantan's statement, it does, however, as well as Gerbe's numbers, point in the direction which was to be expected, according to my theory, discussed in the above. I have, indeed, had an opportunity of investigating some Dutch oysters from Ooster-Schelde. These oysters were partly investigated at the end of March 1923; we had then to do with oysters of the year 1921; that is, they were at that time at the beginning of their second summer. Among 40 individuals, which were objected to a more thorough examination, there were 17 with well developed large eggs which could be detected without the aid of sections. Individuals at the female stage are thus rather frequent among Dutch oysters of not quite two years, whilst they are only exceptionally to be found among oysters in the Limfjord of the same age. Among 30 Dutch oysters of two years, which were examined in June 1922, there were 18 females, likewise a much higher number than is found in the Limfjord. As mentioned above, Hoek (1883 P. 489) found in Holland among 190 oysters 49 with eggs and 31 with fry, also numbers exceeding those in the Limfjord. Later, Hoek (1902 P. 174) has also studied the question and found 49 females among 130 individuals, of which only 17 were mentioned as „sterker mannelijk ontwikkeld", whilst 11 were in distinct transitory stages, and 53 had undeveloped sex organs. The latter were certainly for the greater part animals which had spawned, so that these numbers may seem to indicate that a very great part of the stock spawns in a single summer. According to Hubrecht, (1884 P. 379) the minimum temperature in Ooster-Schelde is rarely less than 17°—18°, from the end of June to late in August, thus it is somewhat higher than in the Limfjord. All my own observations and what I have obtained of information, concerning the spawning of the oyster, seem to confirm the influence of the temperature on the egg-development, of development the female stages proper.

In order to obtain further confirmation of this idea I made some attempts of promoting the development of sex cells outside of the spawning period in artifici-

ally heated aquaria. These attempts, however, met with several difficulties. First of all the experiment can only be carried out with a rather scanty number of individuals, as no more than 3—4 oysters can be kept alive, even in rather large aquaria. Further it proved most difficult to keep the animals alive for more than a few days at higher temperatures. At lower temperatures, i. e. below 14°—16°, I succeeded in keeping them alive, and at temperatures of about 10° I have been able to keep oysters for many months. Through the kindness of Professor Aug. Krogh I was allowed room for the aquaria in the Laboratory of Zoophysiology of the University of Copenhagen from December 1921 — March 1922, and Prof. Krogh moreover was kind enough to assist me in different ways at the establishment of the heating apparatus. The aquaria were heated by steam which was led through the aquaria in leaden tubes; the supply of gas to the lamp, which heated the reservoir in which the steam was developed, was regulated through a regulator lowered into the aquarium, according to a similar principle as that employed at thermostats. In this way the temperature could be kept constantly at 22° in one aquarium, at 28° in another. As said above, I did not succeed in keeping the animals alive for any length of time, as it proved impossible to make the oysters feed on the nourishment with which they were supplied, decaying and putrefied grass-wrack *(Zostera)*, as they do not do so in the nature at this time of the year. Most probably the kind of food had nothing to do with this, for in the spring there was nothing to prevent the oysters in aquaria from feeding on exactly this kind of nourishment. It was certainly, among other things, this question of nutrition which was at the bottom of the scanty result of my experiments, concerning these facts. As it is impossible to obtain any definite knowledge as to the state of the sex organ of an oyster without opening, i. e. killing the animal, it was, of course, impossible to find out which was the state of the sex organ in the animals when they were placed in an aquarium, and as they may, as said above, also in the winter be found at all stages, a later investigation of the organ would not yield any proof worth mentioning. In order to obtain a reliable result, the animals must be prevailed upon to produce eggs or larvæ; this does not namely occur in the nature at this time of the year and would consequently be due to the influence of the temperature. In a single case I did succeed in making an oyster, placed in an aquarium with a temperature of 28°, discharge some eggs $^{14}/_{12}$; it had then been in the aquarium $^{29}/_{11}-{}^{6}/_{12}$, at a temperature of 14°—16°, $^{6}/_{12}-{}^{8}/_{12}$ of 22°, and $^{8}/_{12}-{}^{14}/_{12}$ of 28°. This result, together with observations from the nature, indicate that the egg-development is subjected to the influence of the temperature. Also in some other cases a rather advanced egg-development was observed in oysters having been kept in the heated aquaria, but this may, as mentioned above, also be found in the nature in the winter, and as it was not possible to experiment with a sufficient number of animals for a comparison of the proportion in numbers to be undertaken, no consequence can with certainty be drawn from these cases, even if they point to the influence of the temperature. These

experiments in aquaria do, however, prove that the high temperature alone is not sufficient, a suitable nourishment is also needed. If the development of sex cells is accelerated through a very strong heating, death evidently ensues. In the nature the problem of nutrition will hardly be of so much consequence in this connection [1]) as the decaying process and the formation of detritus and nannoplankton are no doubt promoted with the temperature, so that the quantity of nourishment is increased. The combination of a high temperature and a scanty nourishment therefore is not likely to be very frequent in the nature, and we may consequently take it for granted that in the nature it is mainly a question of temperature, whether much or only little fry is produced. Among the authors having supposed a sex change to take place in the European oyster, Davaine is the only one who has particularly taken into consideration the factors which are eventually effecting this change. He mentions (1853 p. 29) both nourishment and temperature as obvious possibilities, especially emphasizing the latter; he does, however, only mention them as possibilities, without giving further reasons for his supposition, and seems besides to attach special attention to the variations in the temperatures. He evidently is of opinion that a strong variation in the temperature will result in a change of the sex; this is, however, only the case in so far as a variation, tending towards an increase in temperature, is concerned. Finally, it ought to be mentioned that Hoek indicates as a possibility that the nourishment may be of influence to the proportion in % between males and females. As stated above, it can hardly be denied that abundant nutrition is a necessary condition for the development of sex cells, and that the nourishment so far is of great importance, but, according to all my observations and experiences, I must suppose the direct influence of the temperature to be the definite factor; thus it is not the more ample development of nourishment, caused by the high temperature, which counts. The acknowledgment of a direct influence is the only means of explaining, f. inst. that the spawning period sets in at a higher degree of heat when the temperature has increased more steeply in the spring; the many small variations in the spawning, even within an area as limited as the Limfjord, which has besides in most of its localities an ample supply of nourishment, yield the same proof.

What counts is not, as said above, the surpassing of a certain limit of temperature. Authors have often been inclined to speak of definite limits of temperature, when the date for the laying of eggs of an animal was concerned. It will certainly in many cases turn out that the surpassing of a limit is of no consequence. What does count in the case of the oyster is evidently the influence of temperature

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[1]) In a single case I had an apportunity of making such an observation. Among the oysters which were placed in the embanked Klovvig, all those on the western side (the lee side), in quite low water, died off. In the calm low water the temperature was undoubtedly too high in proportion to the amount of nourishment. These oysters consequently had no contents in their intestine, in contradistinction to those from the eastern side.

on the rate of development. It is, therefore, that it takes more time for the eggs to develop at a low temperature. The process is, however, carried through, although more slowly; this is the reason why oysters do not spawn until late in the year in cold summers, and why the intervals between the spawning periods are the longer, the colder the summers. The more heat the water acquires, the quicker the eggs are developed, and if only little heat is procured the proceeding is very slow, at low temperature imperceptible, wherefore, apparently, no development at all of sex products is taking place in the winter. It is to be supposed that the processes are indeed effectuated, the rate of reaction only being so exceedingly slow that it cannot be stated. The whole picture entirely recalls certain chemical processes in which the rate is in the same way dependant on the temperature, so that a decrease in temperature affects the rate so strongly that the processes are practically, although not theoretically, stopped.

The question which was presented as the first and most important of this investigation was the following: Has the temperature any influence on the spawning proper? When the oyster year is bad, is then one of causes, that too little fry is produced? These questions must absolutely be answered in the affirmative. An important cause of the scarcity of oysters in cold years is that the females are too few and producing an insufficient number of eggs. In the above I have tried to explain, how and why the temperature has this influence which is so closely connected with the sex change. Through this explanation the problem has not, of course, been definitely solved. Several factors now interfere, and it depends on these latter factors whether a year of ample spawning will also turn out a good oyster year. We cannot take it for granted that an ample production of pelagic fry will necessarily result in an ample stock of oysters, even if it is, of course, the most important qualification for obtaining this result.

III.

Influence of the Surrounding Conditions on the Pelagic Larvæ.

We shall now pass on to discuss, in which way and to what extent the egg and the pelagic larvæ are subject to the influence of temperature and other surrounding conditions. After having been spawned, the eggs remain, as we know, for some time in the mantle-cave of the mother animal in *Ostrea edulis*, where they develop from the first stages of segmentation to that of larvæ. Until the larval stage, the eggs appear as a white mass accounting for the indication "white sick

oyster"; when the larval stage has been reached, the mass assumes a bluish-black colour, on account of the strongly pigmented intestine shining through these, besides quite transparent, larvæ, wherefore we speak of "blue-sick oyster".

At the above mentioned experiments with oysters with pierced shell I also had an opportunity of observing the duration of these stages. The development from egg to larva lasts 3—4 days; the time which the larvæ spend in the mantle-cave 5—6 days, in other cases they leave it swimming already after the lapse of 2 days. In the first cases, which were observed about $^{20}\text{-}^{25}/_{6}$ the temperature was 14°—16° C, in the last case which was observed $^{24}\text{-}^{26}/_{7}$ in the same year, the temperature was 18°—20° in the tank in question. Thus the temperature seems to be of influence to the growth and development of the larva, even during the period which it spends in the mantle-cave of the mother animal, so that this "blue-sick" period becomes the longer, the lower the temperature, as the larvæ are then developing much more slowly.

In the literature I have not been able to find any information concerning the duration of the above named stages; whereas the free-swimming pelagic stage is amply treated in the literature. The papers are, however, mostly giving descriptions and discussing the morphology of the larva, as to the investigation of the biology of the larva proper there are, as far as the European species is concerned, only two papers at hand, those by Hagmeier (1916 p. 223) and by Mazzarelli (1922 p. 151). Hagmeier especially demonstrates the pelagic stage to be differing in duration and varying according to the temperature, so that it lasts from 14 to 10 days at a temperatnre of 18°—20°. At lower temperatures he supposes the pelagic stage to last still longer, at higher still shorter. The investigations of Mazzarelli have been made in the lake of Fusaro in Italy, and he has arrived at similar results, the duration of the pelagic larval stage being about 14 days at a temperature of about 17°, somewhat longer (17—18 days) at about 16°. The growth of the oyster larva is considerably increased in the course of this period, according to investigations of Hagmeier, it was 0,17—0,21 mm in length, at the beginning of the pelagic stage, whilst it was 0,27—0,31 mm when it attached itself. In contradistinction to this, Mazzarelli states the length to be 0,20 mm, shortly before the attachment. As regards the American oyster *(O. virginica)* a few more investigations of the biology of the larva are at hand, especially of the attaching process (Brooks, Ryder, Stafford, Thurlow Nelson a. o.). In this species the larval stage is of rather long duration, at Canada it is stated to be of more than a month, but attention must be called to the fact that this oyster species is, particularly as far as the breeding conditions are concerned, somewhat deviating from *O. edulis*. It is of separate sexes and the fertilization, the segmentation of the eggs as well as the development of the first larval stage, take place freely in the water, further the larvæ are of more considerable dimensions (0,35 mm) when they attach themselves. Yet what we gather from the literature, concerning these facts, also points to a similar influence of the temperature.

In the Limfjord the temperature since 1914 was only rarely, and not for longer periods, 18° C or more, it is, therefore, to be supposed that the growth of the pelagic oyster larvæ has been proceeding rather slowly during these years. My observations also seem to confirm this supposition, in all respects. Every year pelagic larvæ have occurred, in accordance with the yearly occurrence of a certain number of spawning oysters. The period at which pelagic larvæ have been present in the Limfjord is in exact connection with the above mentioned breeding periods, so that in most years we have been able to find oyster larvæ in the plankton in the first days of June, in 1921 already in the last days of May, in 1923 not until the beginning of July, and in the course of all the summer they may be found till the end of August. It was stated first that, as a rule, the larvæ were very few in number during these years, compared with the other lamellibranchiate larvæ extremely few. A very careful investigation of the plankton sample was most often necessary in order to find even a few specimens. This is in good agreement with the relatively small number of breeding oysters. On a few occasions I have met with a somewhat larger number of larvæ. On $^{24}/_{7}$ 1923 150—200 oyster larvæ were found repeatedly in different places, by a haul with plankton net of 2—3 minutes in the surface. In this latter year, there had been a short but very warm period (18° or more) about the middle of July, and, on account of the early summer being abnormally cold, the commencing of the breeding time had been put off till July. We may, therefore, suppose that relatively many oysters had been spawning at this time of the year. Further, what seems strange is that the larvæ generally found in the Limfjord are very small; although I have had an opportunity of inspecting several hundreds of larvæ during these years, at different times and from different localities, I have only met with few which were more than 0,₃₀ mm in length, and in the Fjord I have only seen a single oyster larva which had acquired its full length, 0,₃₇ mm. This is certainly to be explained like this that only few of the larvæ, produced under the conditions of temperature predominating during these latter years, have been able to obtain their full development. On the other hand, it is excluded that a certain temperature is needed for the larva to reach its full size and attach itself; for if that were so, no larva could ever become an attached oyster. And it has not been so; there is not a single year since 1914 in which some oysters did not attach themselves. This is evident, among other things from the fact that in the following years we meet with young oysters which cannot of course be more than one or two years old, and as we have had the same experience every year up to 1924, we may conclude that a certain number of oysters have attached themselves every year. If we compare with the quantity of the present stock, it is not the question of a great many oysters, but in definite numbers it is, nevertheless, as far as the Fjord is concerned, rather large quantities, no doubt at least a few millions every year, judging by the number of small oysters which are taken. Thus as some oyster larvæ reach their full size, attach themselves and become adult oysters in spite of the low temperatures, it is out of the question that

a certain temperature is needed for the completion of the development. The small number of large larvæ found is certainly due to the rate of growth being strongly decreased, as supposed by Hagmeier. The pelagic stage consequently becomes of long duration, which further implies that almost all the larvæ die before reaching the size when they attach themselves. It is evident that the longer the pelagic stage, the greater the number of larvæ ruined. This means that of the few larvæ produced in the Limfjord, under the conditions of temperature predominating there these last years, by far the greater part is ruined, before they have had time to reach their full size. Only very few of the beforehand scanty number of larvæ grow and attach themselves, and thus become the small, yearly increase of later years. If we take into consideration how extremely fertile the oyster is, according to Möbius every large oyster produces about one million of larvæ, it is easily understood that a certain number of attached oysters may be produced, even if only a few million oysters spawn, and the greater part of the fry is lost.

Through the experiments, made by the Director of the Oyster Company in the summer 1923 for the purpose of producing oyster spat in the tanks, I further had an opportunity of confirming the above named observations. In the first days of July, when the daily minimum temperature in the tanks rose to 20° C, a great number of pelagic larvæ were produced and were quickly increasing in growth, so that larvæ of 0,26 mm, i. e. almost full-grown, might be found $^{22}/_{7}$. On $^{18}/_{7}$ a change in temperature however occurred, reducing the temperature to about 16°. The larvæ were now checked in growth and gradually died off, no doubt on account of the abnormal plankton conditions in such tanks. No larvæ at all had attached themselves, as they all died off before obtaining their full size. An observation, which is sometimes put forth in the literature, the last time by Leenhardt (1923), is the following that in cold summers more larvæ attach themselves in the nature than in tanks, which is, indeed, the opposite of what might be expected, the temperature being as a rule a little higher in the tanks than in the open waters. This is certainly among other things due to the fact that the death-rate of the larvæ is under these conditions rather high, on account of infections and competition for nourishment from organisms which are often developed in abnormal quantities in such isolated localities. During the experiments at the Limfjord, an abnormal quantity of *Nematodes* and *Harpactidæ* were f. inst. developed. It is, therefore, of particular importance to the breeding of oysters in tanks that the temperature is kept high enough for the growth to be rapidly finished, before death overtakes the larvæ. That no result was obtained through the experiment in 1923 was, at any rate, due to the fact that the larvæ died before having completed their development. The bottom of the tanks were completely covered with shells of dead larvæ, and among these not a single one was found to be more than 0,26 mm in length.

The pelagic larvæ are of course subject to influence from other sides than

the temperature, an ample supply of nourishment is f. inst. an indispensable condition for a high growth-rate to take place. Also the salinity is of some consequence, even if these larvæ are able to stand some variation. There are, as we know, oysters in the Limfjord, in the western part of the Nissum Broad, where the salinity is about 32 ‰, as well as in the mouth of Skive Fjord, where it is about 25 ‰, so here we have a proof of their capacity for enduring variation. In aquaria with a salinity of 25 ‰ I have also seen oysters spawning. Even sudden and strong variations do not, at least not immediately, kill the larvæ. I have managed to keep them alive for 8 days in aquaria with only 23 ‰ and 19 ‰, they have lived 3—4 days in water of only 16 ‰. Similar observations have been made by C. G. Joh. Petersen (1907, p. 51). It is also excluded that sudden reductions in temperature directly kill the animals; they may be kept for a long time in aquaria with a temperature of about 12°—13° C; they do not die but their growth is checked or at any rate proceeding very slowly, which is the reason why so few larvæ attach themselves in cold summers. Still there are a few which do so, those that are lucky enough for surviving the pelagic stage which is in such summers of long duration.

I therefore am of opinion that Hagmeier is right in supposing that the growth-rate of the oyster larvæ is strongly reduced at lower temperatures i. e. below 16°—18°, and that it is to this condition that we must look for an explanation of the fact that in cooler summers the fully developed oyster larvæ in the Limfjord are so strikingly few in number and, consequently, the number of oysters attaching themselves astonishingly small, even if a certain part of the stock spawns.

Thus we see that in two respects the temperature is of considerable, even decisive influence to the breeding of the oyster. At higher temperatures more fry is produced, and this fry become adult oysters in many more cases than at lower temperatures. In both cases the influence of the temperature tends to the same result, in both cases the influence of the temperature is of the same kind, as it is not the question of a fixed limit to be reached. The higher the temperature,[1]) the more fry and the more oysters, the lower the temperature the fewer fry and oysters. Thus good and bad „oyster years“ do not make two sharply defined contrasts, but according to the variations in temperature every possible transition is found besides. In one year a rather large part of the stock will spawn, in another year a smaller one, in one year many larvæ reach the adult stage, in another year only few. In the following chapter I shall try to demonstrate how this view of the breeding conditions of the oyster may serve to explain the fluctuations in the stock of oysters, as well as different facts concerning the geographical distribution of the oyster.

[1]) This does not mean, however, that the spawning will increase infinitely together with the temperature. Many things, such as experiences from the spawning basins in Norway as well as my experiments in aquaria, indicate that at very high temperatures (up to 30°) nutrition difficulties will arise to counteract the egg-development. On the other hand, at quite low temperatures (10° and therabout) the processes of egg-development become so slow that they practically cease.

IV.

Fluctuations in the stock of oysters in the Limfjord.

Since oyster fishing was started in the Limfjord in 1852 we have in the statistic enumeration of the number of oysters taken a means by which to form an opinion of the quantity of the stock of oysters. The statistics were published till 1906 by C. G. Joh. Petersen (1907, p. 19); as for the later years the informations are found in the records concerning the oyster fishery (Lunn 1916, Spärck 1921). From these statistics it appears that in the first years only few oysters were taken, then the fishery was increasing towards the end of the sixties, culminating in the years 1871—74 with above 7 million of oysters taken yearly, the yield then began decreasing and in 1885—86 it was less than 1 million. The fishery now was closed and again taken up in 1890—91, partly by other fishing methods, and from now only $^1/_2$ million oysters were fished yearly; this yield gradually rose in the course of years, slowly mounting to above 1 million. In 1910 another fishing method was introduced, the yield now being raised to $3^1/_2$ millions and culminating a second time in 1915—16 with above $5^1/_2$ millions. Since that time the fishery has again been reduced, in 1922—23 it was $2^1/_2$ millions. Thus we see that a strong fluctuation in the yield has taken place with two culminations in the first of the seventies and in 1915—16.

As regards the conditions of temperature of these periods, information of the temperature of the surface water in Oddesund may be had from the Danish Institute of Meteorology as far back as to 1893, and the air temperature in Vestervig near the Limfjord is known as far back as to 1874. Unfortunately therefore nothing can be stated with certainty concerning the temperature in the Limfjord in the last years of the sixties, and it is on the whole far from easy to draw any definite consequences from the air temperature to that of the water. If we inspect the diagrams from later years it is however evident that the temperatures of the air and the water mainly agree. As to the temperatures of water I have already several times mentioned that since 1914 we have generally had low temperatures, only for shorter periods a temperature above 18° C; 1917 is the year which comes the nearest to 1914. If, on the other hand, we turn to the years before 1914 we had 3 warm summers in 1910, 11 and 12. (Fig. 11—18). According to this it is easily comprehensible that in the years about 1915 we must have had a very large stock which became much reduced afterwards. What is worth noticing is that a single warm summer as in 1917 apparently is of no great effect; whilst a series of warm summers as in 1910—12 and 1914 were of great consequence to the increase of the stock. It is in exact accordance with my view of the function of the sex organ, discussed above, that a single warm summer is not very effective, as the egg-development is often accomplished in the year previous to the spawning process.

1910

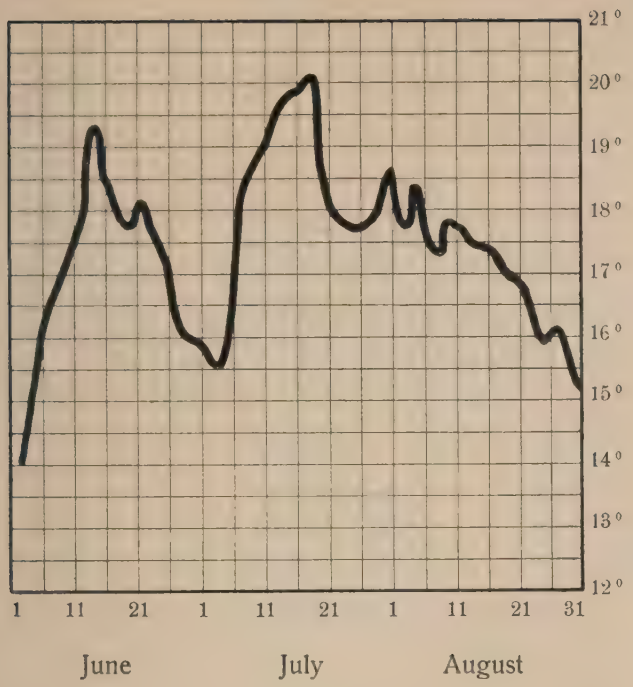

Fig. 11

1911

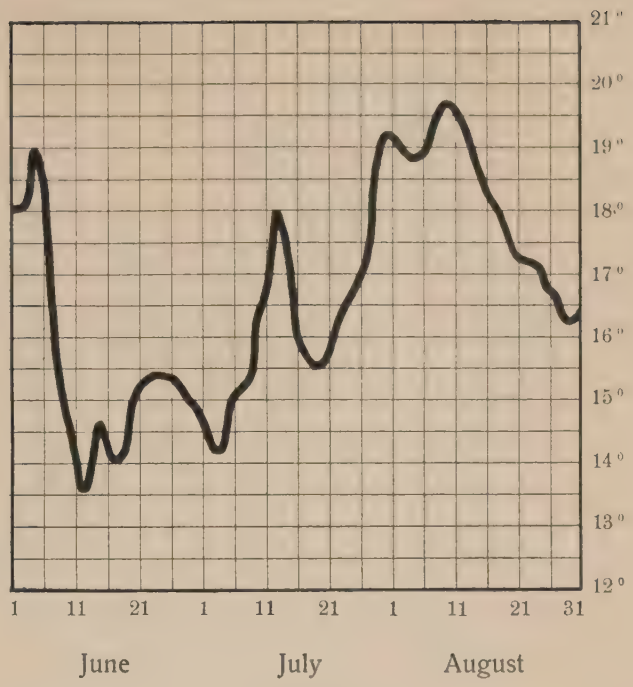

Fig. 12

1912

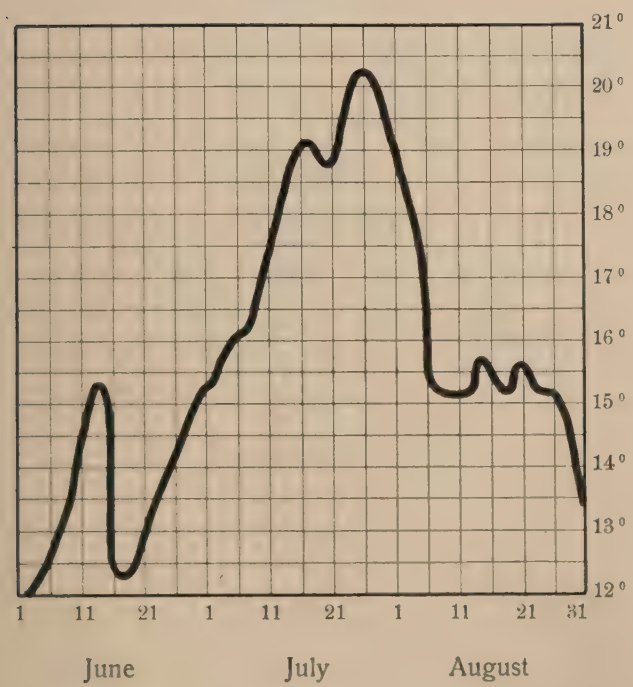

Fig. 13

1914

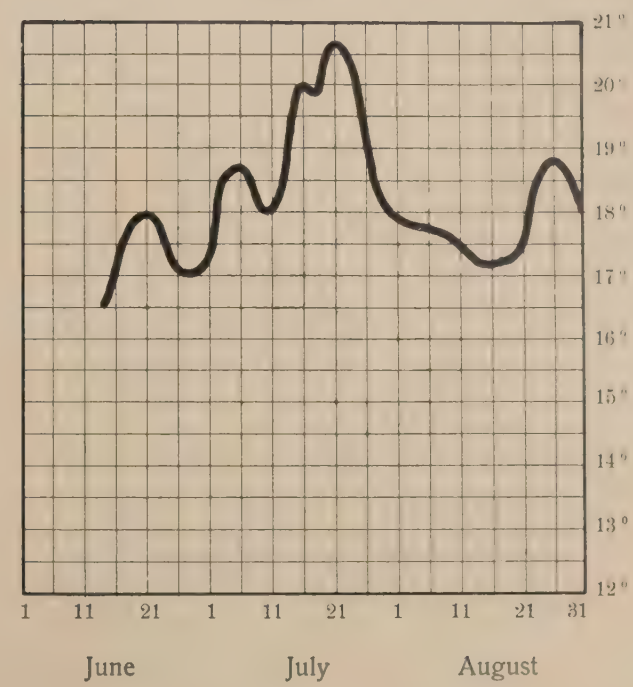

Fig. 14

Fig. 11—14: Surface Temperature of the water at Oddesund (Limfjord) June—Aug. 1910—12 and 14.

1910

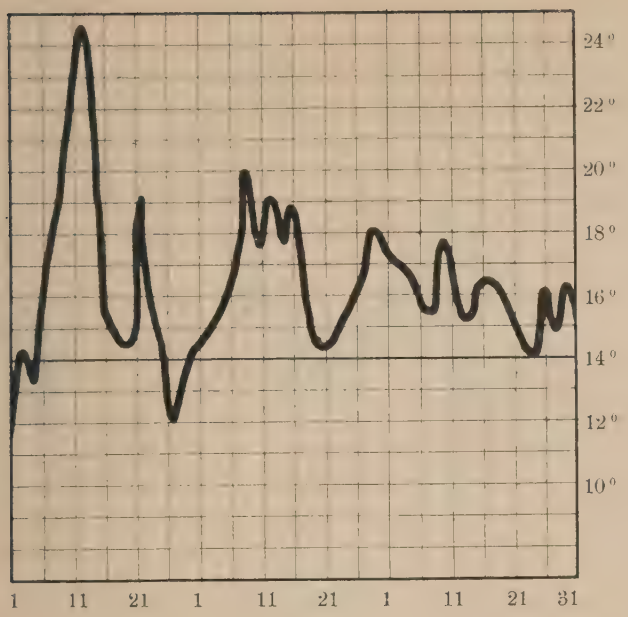

Fig. 15

1911

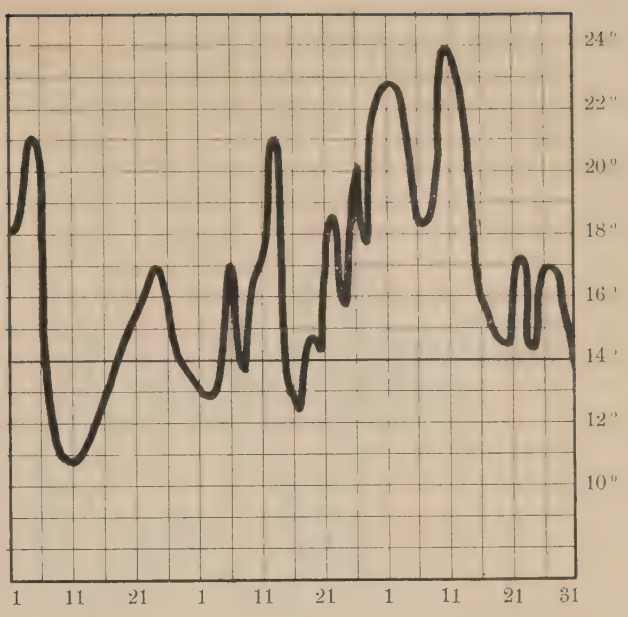

Fig. 16

1912

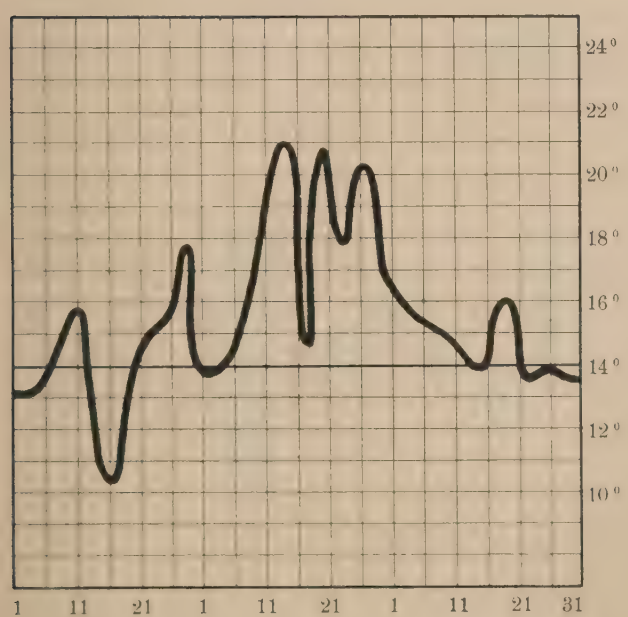

Fig. 17

1914

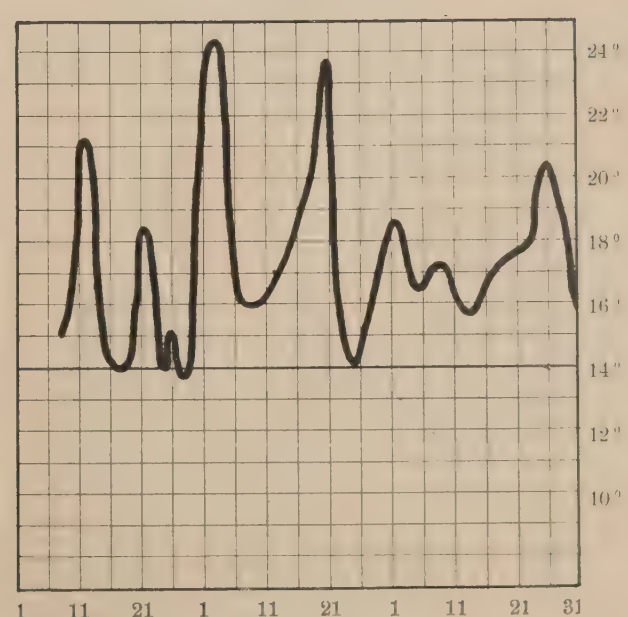

Fig. 18

Fig. 15–18: Temperature of the air at Vestervig near the Limfjord June—Aug. 1910–12 and 14.

1885

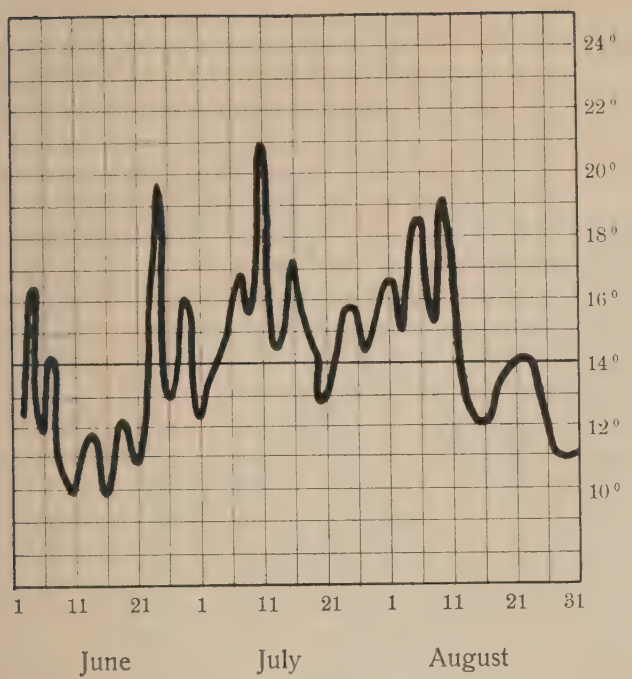

Fig. 19

1886

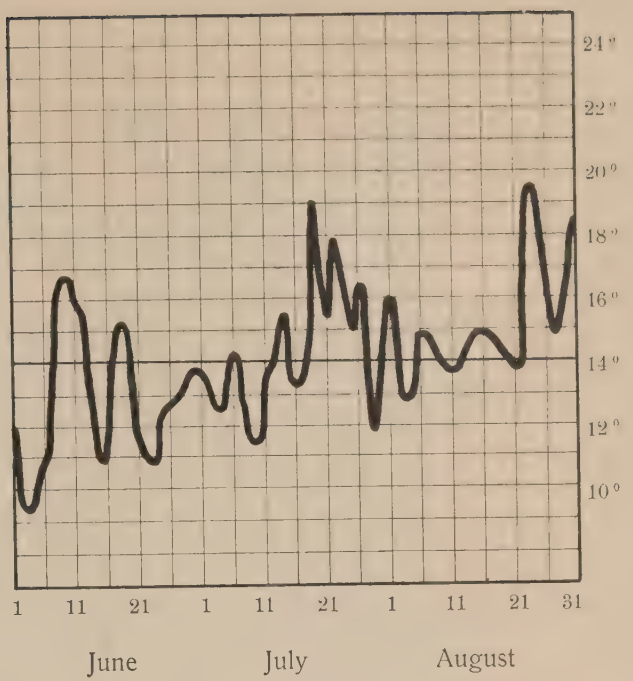

Fig. 20

1887

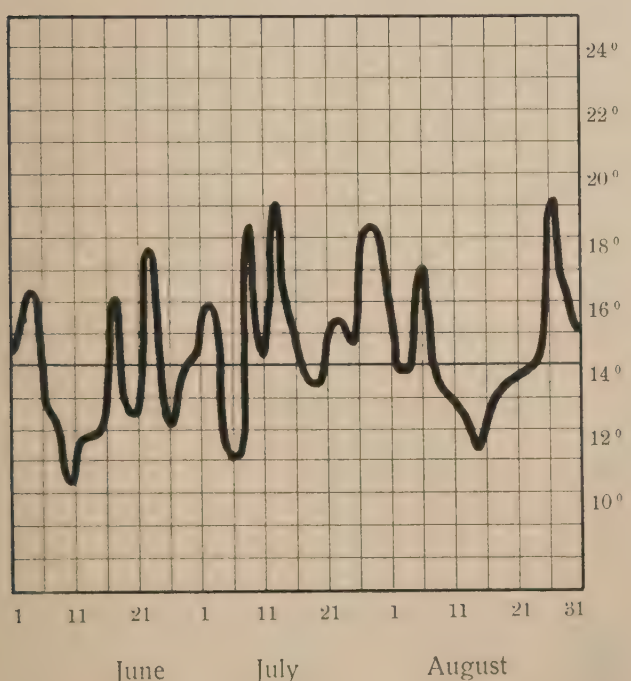

Fig. 21

1888

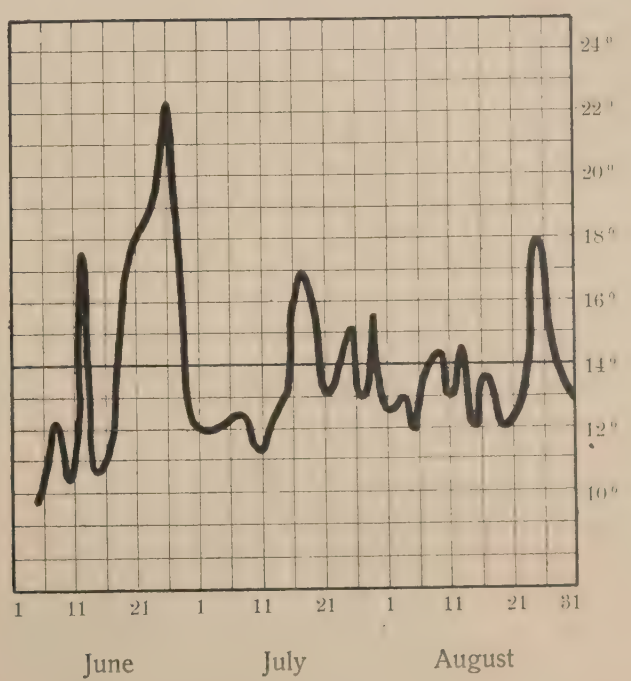

Fig. 22

Fig. 19–22: Temperature of the air at Vestervig June—Aug. 1885—88.

The number of eggs spawned is, therefore, not only dependant on the temperature of the summer in question but also to some extent of the one before. An ample egg-development in one summer will naturally result in a rich spawning in the following, and vice versa if the preceding summer was extremely cold. We therefore understand that a cold period as the one we have had since 1914, except for a single warm summer, must be of decisive and disastrous influence to the quantity of the stock of oysters. We likewise understand why the stock of oysters was increasing in the nineties and the beginning of the twentieth century. There were several warm summers successively (1896—97 and 1899—1901). If we look at the conditions of the eighties there were only few warm summers, especially in 1885—89 there was a long and very cold period, which makes it quite clear why the yield was so scanty in the first of the nineties (Fig. 19—22). Also the last of the seventies was partly cooler than the nineties, and the years about 1910 partly without continued warm periods, so that also here we find the explanation of the great reduction during these years. The reason was that the increase did not in these years suffice for making up for the reduction through the fishery and particularly the mortality which is extremely great in oysters. As also mentioned by Orton (1923 p. 1) zoologists have certainly been inclined to undervalue the natural mortality of these animals. The oyster has, as we know, many enemies and is also in other ways exposed to death (frost, lack of oxygen a. s. f.), so that the mortality must be supposed to be very great. I shall not enter into any further discussion of this question but be content to mention that from my observation of the number of shells of oysters probably recently dead (in which case the shells have no inside coating of Balanidæ, tubes of Annelidæ, Ascidiæ etc.) I have come to the conclusion that the annual death rate of oysters amounts to almost 20 % of the stock. In many places where spat is purchased and transplanted an annual death rate of 20 % of the stock and sometimes even still higher, up to 25—30 % is reckoned with. Thus it is evident that an ample production of fry and spat is needed in order to keep up a stock of oysters. It is likewise easily understood that even a small reduction in the production of fry, i. e. a relatively slight decrease in the temperature below 18—20° may be fatal to the maintenance of the stock, especially if the decrease is prolonged during many years. It is, therefore, a matter of course that for the development of such a large stock of oysters as we had in the Limfjord in 1910—20, a series of warm summers with increased production of fry and increased attachment of spat is required.

As regards these last years (since 1912) we have, through the statistics of the fished spat, a means for judging of the fluctuations of the stock. By spat is meant in the statistics such small oysters as are dredged together with the large oysters not sold along with these latter but relaid on the artificial beds. These small oysters are for the greater part young individuals of 1—3 years, although it must be acknowledged that among these latter, especially from the eastern part of the Fjord, there are some small but old oysters which have not, for some reason or

other, obtained their normal size. In the eastern part of the Fjord, where the salinity is sligther, this is, as already said, not uncommon, no doubt on account of this smaller degree of salinity. It is only after 1912 that the gathering of these small oysters has become a matter of interest, wherefore no statistics of the number of these animals are at hand before this year.

Synopsis of the number of small oysters dredged.

1912—13 1,273,000	1915—16 3,461,000	1920—21 1,408,000
1913—14 1,273,000	1916—17 2,499,000	1921—22 1,193,000
1914—15 2,632,000	1919—20 1,409,000	1922 - 23 394,000

From this synopsis it appears that the fluctuations in the number of small oysters dredged are as considerable as those mentioned above, with reference to the larger individuals. Our attention is especially called to the great increase in the years 1914—16 after which the number is again decreasing. 1917—19 are not included as no dredging of greater dimensions was undertaken on the natural beds, on account of the scanty supply of petroleum caused by the war. The increase in 1914—16 was undoubtedly due to the warm summers of 1912 and 14. It is our experience that the increase in the amount of spat only appears in the number of dredged small oysters 1—2 years later, not already in the winter immediately ensuing the spawning period. This has for reason that the small oysters are often so diminutive in the first winter that they are either overlooked or pass through the rather wide meshes of the oyster dredges. This is why we have the great increase later on. But we also notice that especially the summers 1912 and 1914, above all the latter, play a very prominent part in the synopsis, much more so than those of 1910 and 1912. As far as the summer of 1914 is concerned, the explanation is near at hand, the temperature of the water being much higher than in any of the summers observed before then (i. e. since 1893), and besides this, the summers previous to 1912 and 1914, to wit those of 1910—11, were also rather warm. In accordance with what has been discussed in the above it is to be expected that the last summers of a warm period will be particularly spawn-producing. Since 1916 the number of spat has been constantly decreasing. In 1920—21 there was still taken more spat than in 1913—14, although these latter summers were a little warmer. This may be explained by the effect of the warm summer 1914 lasting far onwards through the years, by a greater number of oysters having spawned in the following summers in spite of the temperature, and by a certain number of slowly growing individuals from 1914 appearing as spat in the ensuing years. Finally the summer 1917 was, as said above, rather warm, 1918 was the warmest but two after 1914 and 1917, and it is, as we know, especially the spawn from 1917 and 1918 which occurs in 1919—21. After 1921 the decrease is gradually accentuated, and in 1922—23 the number of young oysters dredged is strikingly diminished. Since 1918 we have not had a single only passably warm

summer, the summers 1919—22 must even be designated as uncommonly cold, with temperatures generally about 14°—15°. As before maintained by me, it is especially in such a long period of low temperature that the number of spat will decrease, above all towards the end of the period, here we have part of the explanation of the considerable decrease in 1922. Another reason is the decrease of the stock of oysters in the Limfjord which is due to its having been only scantily renewed. For these reasons, and because only a small % of the oysters are spawning in the cold years, and only a small % of the fry produced are thriving, the number of oysters attaching themselves becomes extremely small. This number will however, all other conditions equal, be in proportion to the quantity of the stock. When a cold period follows on a warm, the stock will decrease in number and the spawn likewise, year after year, till an increase is again taking place in some warmer years. Thus the enormous decrease in the number of small dredged oysters in 1922 is also due to the stock from 1910—14 commencing to disappear about 1920, and what is left is a stock produced by the scanty, constantly decreasing spawning since 1914. This essentially smaller stock spawning under the same conditions of temperature as those of a greater must needs result in a much smaller number of spat. Finally I shall call the attention to the fact that what is designated as spat is a matter of estimate, and this estimate may vary somewhat from year to year. During the last years with a smaller yield of the fishery there has certainly been a tendency to bring into the market younger oysters than in earlier years, when large oysters were abundant. The decrease in 1922 is perhaps not quite so great as it will appear from the synopsis, but in the main this latter does, however, undoubtedly present a correct image of the whole proceeding.

Also in some other respects some information of interest to the biology of the oyster may be obtained from the statistics of the small oysters. It namely appears that in the eastern part of the Livø Broad (east of Livø) and in the Risgaard Broad small oysters are caught in relatively greater numbers than in the remaining part of the Limfjord; I have formerly mentioned this fact in the above named record to which I must refer as to the exact numbers. This may have for explanation that the temperature in this inner part of the Fjord which is outside of the stream current proper, must be supposed to be a little higher. Unfortunately no regular observations of temperature are at hand from this part of the Fjord, so that I have to refer to my own observations from my visits to the waters in question. On the $^{6}/_{8}$ 1920 at 1 o'clock the temperature at the mouth of Skive Fjord was 16,2° C, in the surface at Nykøbing, Mors, it was in the afternoon of the same day 15,5° and at Oddesund the morning temperature on this same day was 13,8°. On the $^{6}/_{10}$ of the same year the temperature N. W. of Fur was 10,9°, at my arrival in Nykøbing a few hours later it was 10,6° there. On $^{14}/_{9}$ 1922 at 11 a. m. in Lovn's Broad the temperature was 15°, at noon in Hvalpsund 14,8°. at $1^{1}/_{2}$ p. m. at Rindgrund 14,8°, at 3 p. m. at Løgstør 14,6°. On $^{12}/_{9}$ 1923 the temperature was

at Hvalpsund 13,8°, at 11½ a. m. in Fursund 13,6°. All these numbers indicate that the temperature is a little higher in these inner parts of the Limfjord than in the outer parts, and especially higher than in the Nissum Broad.[1]) It is only the question of ½°—1°, but it seems to be sufficient for an increasing in the quantity of spat. It ought besides to be noticed that in these parts of the Fjord with lesser salinity there are some more adult oysters among the so-called spat which may, therefore, to some degree, but not fully, serve as a satisfactory explanation. The main part of the spat is namely here as well as otherwhere really young oysters.

Finally I shall speak of the numeric proportion between large and small oysters. Setting aside the waters between Livø, Fur and Himmerland in which the small oysters caught 1915—17 were in the majority, it is always the large oysters which are the most numerous. If the stock of a year of abundant spawning and attachment such as 1914 was multiplied, we might suppose that the small oysters would by far prevail upon the large oysters in the following years. This has not, however, been the case, only in a single part of the Fjord the quantities were, as said before, equal, in one place the small oysters even predominating. This seems to me to prove that the stock can hardly have been redoubled, not even in so good a summer as that of 1914. Nothing else could indeed have been expected. For what was it that happened in 1914? It happened that some oysters, which were otherwise only going to spawn in 1915 or 1916, did spawn already in 1914 together with those which would have done so even if the summer had been a cold one. Theoretically seen, the best thing which may occur in such a summer is, of course, if all oysters spawn. Even in a warm summer it must be reckoned with that almost all the larvæ produced by an oyster are ruined, and only a few becoming adults. A redoubling of the stock, i. e. each oyster giving rise to a new one, must therefore be regarded as a very fine result, which implies that almost the whole stock spawns. This is what seems to be the normal state of affairs in the warmest of the Norwegian breeding basins under similar conditions. In the Limfjord on the other hand, such a result is only very rarely to be expected, even in such a year as 1914. It is, therefore, easily comprehensible that of later years the number of small oysters is in relatively constant decrease. In 1915—16 the proportion between large and small oysters was 5/3, in 1922—23 6/1.

If we look at the fluctuations in the numbers of the stock of oysters in the course of the years, we see that in certain periods the yield was considerable, in others scanty. The first named followed on a period of warm summers, the last named on one of cold summers. If we inspect the producing of spat we see that it has been essentially more abundant in warm periods than in cold. Even in very warm years the increase in proportion to the stock does not seem to be considerable, in 1914 not even a redoubling. All this appears to me to confirm

[1]) The synopsis on p. 65 of the temperatures at Oddesund and Aalborg shows exactly the same difference to exist between the western and the eastern part of the Fjord.

my view, stated in the above, of the spawning in the oyster, to wit, that there is no definite division between good and bad spawning years, and that the effects of a single year are extending into the ensuing, wherefore it is more pronouncedly the period than the year which is of the greater consequence. Another reason for this latter statement is found in the fact that the greater the stock at hand the more abundant the production of spat, all other conditions besides equal. We therefore have to do with these long periods with increasing or decreasing stock, periods which are in the main dependant on the summer temperature of the water.

V.

Geographical Distribution of the Oyster.

In our days the common European oyster *(Ostrea edulis)* ranges from the West coast of Norway along the Atlantic coast of Europe into the Mediterranean and the Black Sea. Especially from southern waters a whole series of "species" has been described in the course of time. The establishment of so to say all these "species" is based on variations in the appearance of the shell. The shell of the oyster is, however, highly variable, according to the very great influence of the salinity of the water, the kind of the ground, etc. We therefore meet with a multitude of varying shells in the different parts of the Limfjord, without however being justified in regarding these variations as anything but the result of surrounding conditions. In this connection it ought to be mentioned that young oysters imported from Holland and relaid in Nissum Broad will, in the course of a few years, obtain the same appearance as to colour and shape of the shells as the "native" oysters in the locality in question of the Limfjord. Quite similar alterations may be observed in oysters which are transferred from the inner broads in the Limfjord to Nissum Broad. Great prudence is therefore recommended for the judging of the differences in the appearance of the shell, and there is every reason to believe that a great number of the oyster species which conchologists, especially in the first years of the last century, described from the western coast of France and particularly from the Mediterranean, are nothing but varieties of *Ostrea edulis* due to local conditions. This point of view has before been (adopted by f. inst. Bucquoy, Dautzenberg and Dollfus (1887—98) who maintain besides *O. edulis* only *O. stentina* Payraudeau as a separate species. Before a thorough study of the biology, hereditary conditions and anatomy of these many different "species" has been accomplished it will, however, be impossible to determine their systematic

value. As already said there is, however, much to speak for a considerable reduction of their number. *O. angulata*, the so-called Portuguese oyster with separate sexes, is undoubtedly differing in species from *O. edulis*. Lacaze-Duthiers (1854 p. 217) has stated the above mentioned *O. stentina* to be a hermaphrodite like *O. edulis*, wherefore it may be dubious whether these two forms are indeed different species. According to Bucquoy, Dautzenberg and Dollfus (1. c. p. 23) *O. stentina* is also occurring at Madeira and the Canary Islands. If *stentina* is referred to *edulis*, the distribution of the common oyster is thus extended to include the Mediterranean and the Black Sea as well as the West coast of Europe from the Arctic regions to North West Africa.

It is, however, not the south limit of the distribution of the oyster which is of special interest to this discussion, but the north limit at the West coast of Norway and the boundary line in the Kattegat, as we have here an opportunity of amplifying our knowledge of the influence of the temperature on the distribution of the oyster. As far as the distribution at the West coast of Norway is concerned, we find informations by Nordgaard (1913). The most northward occurrence of the oyster at the West coast of Norway is now said to be at Tjøtta a little S. of 66° N. The stock of oysters along the South and West coast of Norway is however, the basins (Poller) excepted, now very scarce, not fit for any fishing on a larger scale. Judging by informations which may be found in papers by Norwegian authors who have taken up this subject for study (Helland-Hansen, Nordgaard a. o.), the scantity of the stock is mainly due to the small increase. If we study the temperature this is easily comprehensible. According to Jahrbuch des norwegischen meteorologischen Instituts, I have in the following compared the mean temperature of the surface in the months April—August at some Norwegian lighthouses.

Surface Temperature at the Coast of Norway.

		April	May	June	July	August	1914	April	May	June	July	August	1919
Torungen	(58° 25′ N.)	4,5°	8,5°	13,9°	17,6°	17,6°		3,1°	9,4°	11,9°	16,4°	14,0°	
Utsire	(59° 18′ N.)	6,1°	7,9°	11,8°	16,7°	17,0°		4,7°	9,0°	10,8°	13,7°	12,9°	
Hellisø	(60° 45′ N.)	5,2°	7,1°	9,7°	15,0°	16,2°		4,5°	8,1°	9,4°	10,5°	11,5°	
Ona	(62° 52′ N.)	5,9°	6,8°	9,9°	13,9°	14,3°		4,7°	8,0°	10,6°	11,8°	11,9°	
Nordøerne	(64° 48′ N.)	4,9°	6,0°	9,1°	14,2°	13,3°		4,1°	7,1°	10,2°	12,4°	11,7°	

We see from this synopsis that the water temperature of the summer is considerably lower at the Norwegian coast than in the Limfjord. We further observe that oysters are living in waters, in which the summer temperature even in a year as warm as 1914 is as low as about 14° C. At such a low temperature oysters may then be living and spawning[1]), but the stock is extremely small which is

[1]) I do not see much reason for supposing the stock of oysters at the northern part of the West coast of Norway to be due to larvæ having arrived from the southern waters. The conditions in the Limfjord and in the cold basins in Norway prove that oysters are able to spawn at such

what might be expected, according to the conception of the spawning conditions of the oyster, which are stated by me in the above. These oysters very rarely become females, each individual will only spawn few times, perhaps only once in the course of its life, until we come down to temperatures (as low as 10°—12° in the warmest month) at which the oyster larvæ, which might be imagined eventually to arrive here from other waters, do not get time to develop into females; thus they will not be able to spawn, and here we are at the limit of the distribution of the oyster. We now understand that oysters may be living at temperatures lower than those in the Limfjord, and that the stock must thereby be especially reduced; and the scanty stock of oysters found in the open waters at the West coast of Norway, even upwards to North of the mouth of the Trondhjemsfjord, thus becomes easily explicable.

According to Jeffreys (1863 p. 39), the oyster occurs at the Shetlands, though it is not very numerous here nor at Scotland; it is not found at the Færoes. Jensen (1912 p. 11) however states that a quite tiny oyster once was found attached to a *Modiola* shell from the Færoes. It is certainly excluded that this oyster was born at the Færoes. According to Jacobsen (1913 p. 39), the summer temperature in the Fjords of the Færoes seems to be still lower than in the most northern locality where the oyster occurs on the coast of Norway, namely about 8° even in the month of June. According to Ryder (1917) the surface temperature at Thorshavn is in the warmest month 10°—11°, i. e. considerably lower than at the coast of Norway. The above-named tiny oyster must therefore be supposed either to have been carried to the Færoes by the currents, or the *Modiola* to have been attached to a boat. That animals from the South can be carried by currents to the Færoes has been proved this last year by the great numbers of *Sepia* shells which were washed ashore on the Færoes (Spärck 1923 p. 141). But even if something of that kind might exceptionally happen to oyster larvæ, the temperature at the Færoes will most probably prevent the oyster from thriving there, and it is therefore easily comprehensible that, except for the above named specimen, no oyster was ever stated there.

I shall now pass on to discuss another boundary area to the distribution of the oyster, to wit, the Kattegat. Informations concerning the present and former distribution of the oyster in this and adjacent waters have been collected by Nordmann (1903 p. 45). Winther (1875 and 76) and C. G. Joh. Petersen (1888 p. 119) have besides given special attention to this question. According to statements from these two authors, the oyster is nowadays to be found in the Kattegat, partly in the Aalbæk Golf, where oyster fishing was going on towards the end of the

low temperatures, a comparison with the distribution of the oyster in the Kattegat where conditions are homogeneous also indicates that an invasion is excluded. If namely the oyster could be carried so far north in Norway it would be carried more southwards and thus be found further South in the Kattegat than is now the case.

last century, partly S. E. of Læsø and at Anholt as well as here and there N. and W. of Samsø and in the Aarhus Golf. A single newly dead oyster is said to have drifted ashore on the North coast of Fuenen. In the eastern part of the Kattegat the oyster is not found so far South as in the western part, only N. of Göteborg it occurs in fairly large numbers, but a few are said to occur as far South as Varberg (Krogh 1870 p. 41). It further ought to be noticed that in the Kattegat, the Aarhus Golf excepted, the oyster is found at rather considerable depths (about 20 m or more), also that the density of the stock is somewhat scanty, compared with that of the Limfjord, so that the fishing for oysters does not pay anywhere here, and, with the exception of the Aalbæk Golf, no fishing for oysters has taken place in the Kattegat, at any rate not in the last centuries. Winther enters rather thoroughly into the question of the conditions limiting the distribution of the oyster in the Kattegat, and in this connection he emphasizes the temperature and the salinity, however laying particular stress on the latter. In those years no ample and regular hydrographical observation existed with reference to the Kattegat; Winther does not either take up for discussion the breeding habits of the oyster, of which only very little was known at that time. It is, therefore, perfectly natural that he came to the conclusion that all the oysters occurring in the Kattegat S. of the Aalbæk Golf originated from the last named locality and had as larvæ been carried southward by the current to Anholt, the Aarhus Golf etc.

According to Nautisk-meteorologisk Aarbog, I have in the following put together the observations of temperature and salinity for the months of April—August from a few light-ships in the Kattegat. I have chosen the years 1914 and 1919, the first named being exceptionally varm, the last named more "normal". Observations of temperature from the Limfjord (Oddesund and Aalborg) are added for comparison.

Læssøe Trindel.

		1914					1919				
		0 m	5 m	10 m	15 m	21 m	0 m	5 m	10 m	15 m	21 m
April	Mean Temperature	5,8	5,5	5,2	5,3	5,3	4,4	4,2	4,0	3,9	3,8
	Mean Salinity ‰	21,1	21,9	25,7	30,3	32,0	29,2	30,4	32,1	32,7	33,1
May	"	9,9	9,8	9,0	8,1	7,5	10,2	9,7	7,7	5,8	5,5
	"	25,0	25,9	28,3	30,3	31,4	20,5	21,3	26,4	31,4	33,4
June	"	14,5	13,9	11,7	10,0	9,2	13,9	13,8	12,9	12,3	11,5
	"	19,5	20,4	25,9	30,9	32,2	27,1	28,1	30,0	31,6	32,4
July	"	19,1	18,5	16,9	16,1	15,1	16,5	16,1	15,1	14,5	14,0
	"	19,3	21,4	27,3	30,1	31,3	24,1	25,1	28,4	31,1	32,1
Aug.	"	17,7	18,1	17,7	17,2	16,5	14,8	14,7	14,6	14,5	14,4
	"	22,5	23,9	29,2	31,5	32,2	30,4	30,9	31,1	31,7	32,0

Læssøe Rende.

		1914					1919				
		0 m	5 m	10 m	15 m	21 m	0 m	5 m	10 m	15 m	21 m
April	Mean Temperature	5,8	5,7	5,3	5,2	5,0	4,9	5,0	5,1	4,8	4,6
	Mean Salinity ‰	21,4	24,0	29,6	31,5	32,0	28,6	29,3	31,1	32,0	32,3
May	„	9,7	9,6	9,1	7,2	6,9	10,2	9,5	7,7	6,0	5,8
	„	25,7	26,7	29,3	31,0	31,4	21,5	24.0	28,6	30,8	31,5
June	„	14,4	13,3	10,3	8,0	7,9	14,1	13,8	11,6	9,9	9,6
	„	20,0	21,3	28,1	31,3	31,7	21,9	25,5	29,9	31,0	31,7
July	„	18,2	17,5	13,8	12,7	12,3	16,0	15,8	14,6	12,8	12,8
	„	17,3	18,4	27,4	29,6	30,0	22,1	24,0	29,8	30,7	31,3
Aug.	„	17,7	17,3	15,6	15,0	14,8	14,7	14,8	14,8	14,7	14, 6
	„	20,0	21,6	29,5	30,8	31,0	30,9	31,3	32,7	32,1	32,3

From this synopsis of the distribution of temperature and salinity in the northern part of the Kattegat it appears, first of all that the salinity is in the surface often considerably below the minimum (24—25 ‰) at which the oyster spawns in the Limfjord. In order to get constantly and with certainty beyond this minimum we must seek as far down as to about 10 m. In this depth the temperature is, however, much lower than in the Limfjord. Even in the warm year 1914 it was not until the month of August that the temperature rose to 17,7 ° at Læssøe Trindel at a depth of 10 m; at the bottom the temperature was 16,5 °. In Læssøe Rende the corresponding temperatures were 15,6 ° and 14,8 °. In the Limfjord the temperature was in 1914 and 1919 as follows:

		Oddesund	Aalborg
April	1914	7,5	7,6
—	1919	5,4	6,0
May	1914	10,6	11,5
—	1919	11,0	12,2
June	1914	15,6	16,1
—	1919	14,2	15,5
July	1914	19,0	20,0
—	1919	15,3	16,9
Aug.	1914	17,8	18,1
—	1919	13,8	14,7

From these temperatures, showing the average of the temperatures of the surface at 8 o'clock every day of the months in question, it appears that the surface temperature in the Limfjord is a little above that in the northern part of the Kattegat and several degrees above the temperature of the depths in the Kattegat,

where the salinity is sufficiently high for oysters to live there. In the Limfjord where the oyster occurs in rather low water (4—8 m), there is no difference worth mentioning between the temperature at the surface and that at the bottom. We now understand why the stock of oysters must become much more scanty in the Kattegat than in the Limfjord. In the deeper water layers in the Kattegat, to which the oyster must resort because of the distribution of the salinity, the maximum temperature is in the summer only slightly surpassing the surface temperatures at the coast of Norway and like these it also occurs late in the year, we therefore have a stock of oysters of particularly small density like that of the Norwegian localities and for exactly the same reasons. If we proceed further S. and E in the Kattegat, the difference between the temperature here and in the Limfjord is still more pronounced. At the Schultz' bank we must seek down to 15 m in order to reach to a sufficiently high degree of salinity, and we here have a summer temperature which was in July 1914 on an average $8{,}5^{0}$, in August $12{,}1^{0}$; at the bottom the corresponding numbers were $6{,}5^{0}$ and $9{,}8^{0}$. Thus we see that the temperature was here considerably lower than the temperature at the most northern localities in Norway, and consequently it is easily comprehensible that we do not find any oysters in this part of the Kattegat. At Anholt Knob it is also necessary to descend to a depth of 15 m in order to reach the salinity needed; here the temperature was in July 1914 $13{,}1^{0}$, in August $17{,}6^{0}$; at the bottom the temperature was in those months $9{,}6^{0}$ and $14{,}1^{0}$. So here we have temperatures of about the same degrees as those of the most northern localities in Norway, and we understand why even Anholt is stated as the most southern locality for the occurrence of oysters in this part of the Kattegat. At the Lappegrund, in the northern part of the Sound, the temperature was at a depth of 15 m, in July and August 1914 respectively $7{,}4^{0}$ and $12{,}6^{0}$, this is then the explanation why oysters are absent in the northern part of the Sound, in spite of the presence of sufficient salinity and favourable bottom conditions. It is evident that the distribution of the oyster in the deeper parts of the Kattegat does not depend on salinity but on temperature. It is further evident that in depths with sufficient salinity for the oyster to thrive, the temperature decreases southwards in the Kattegat until it becomes lower than the temperature at the most northern localities of the oyster in Norway. As in Norway we therefore have a stock of oysters which is to an exceedingly small degree multiplying itself, the less, the further we proceed southwards in the Kattegat, till gradually we reach to the limit of its range. Thus the supposition of an invasion of larvæ is not needed in order to explain why the stock is so scanty; the conditions of temperature and the influence of these latter on the sex change and the growth of the larva fully account for it.

As said above, Winther (1875 p. 29) states that some oysters were found on large stones in rather low water at the innermost end of Aarhus Bay and Kalø Inlet. The presence of these oysters Winther will also refer to an invasion of larvæ from the Aalbæk Bay. This sounds in advance somewhat unlikely, because

if it were so we could hardly expect them with preference to occur in the inmost part of the Bay. If we do, however, study the conditions of temperature and salinity in the Kattegat, as they have been put together by Jacobsen (1908) after 27 years of observations, it turns out that the direction of the isohalines in the Kattegat is such that the inmost part of the Aarhus Bay has a higher salinity than the outmost part, the main salinity inmost in the bay exceeds 24 $^{0}/_{00}$, already at a depth of 10 m. Apart from the coasts of Læssøe and the east coast of Vendsyssel, there is no place at the Danish coasts of the Kattegat where the salinity reaches so high a degree as in the inner part of the Aarhus Bay. If we turn to the conditions of temperature, the average maximum temparature is 16,5 ^{0} at the surface, 15 ^{0} at a depth of 10 m; this temperature occurs about August 1st, and August 10th, respectively. Thus we see that the conditions of temperature in the Aarhus Bay are also conducive to the explanation of the scarcity of the stock of oysters there; there is no reason for supposing the stock of this Bay to be due to an invasion of larvæ.

According to the charts, drawn by Jacobsen (l. c.) of the direction of the isohalines in the Kattegat we understand that as the isohalines are at the surface passing from S. W. to N. E., the oyster must at lower water go further southwards in the western than in the eastern part. As appears from Nordmann's synopsis (1903) the oyster was also in the Stone Age (the Tapes age cp. C. C. Joh. Petersen 1888 p. 52) to be found further South in the western part of our waters than in the eastern; it was likewise found further South at the West side of the Large Belt than at the East side. This may certainly have its explanation in the isohalines having then as well as now in the Kattegat and the Large Belt the direction from S. W. to N. E., wherefore the salinity of the western side of the waters in question was highly surpassing that of the eastern side. As far as the greater depths are concerned, it is the decrease in temperature which is decisive to the range of the oyster in the Kattegat, whereas in our days, as regards lower water, it is the salinity which is decisive to the range of the oyster in our interior waters as well as in the Limfjord E. of Normands Hage and S. of Hvalpsund.

A further account of the distribution of the oyster during the Tapes age does not come inside of the frames of this work. Only this may be emphasized that what makes the great difference between the conditions then and now is the occurrence of the oyster in quite low water in small inlets and bays at that time. Through some preliminary excavations, made by me in the now elevated sea bottom at Mejlgaard, it was proved that oysters had been living in this bay in the Tapes age at a depth of scarcely 1 m. At the digging in the elevated layers, in a place which was c. $^{1}/_{3}$ m below the highest level of the sea in the Tapes age, it was only necessary to get as far as 70 cm down in order to meet with layers abunding in oyster shells, the depth of the sea, therefore, can only have been at most about 1 m when these shells were layered. In our days we also meet with oysters as far South in the Kattegat as Mejlgaard, but we must proceed to

depths of more than 10—15 m, and the stock of oysters which is able to thrive in such depths is minimal, compared with that which can live in the low warm water. Only this that the salinity in the Tapes age permitted the oyster to live at quite low water in our interior waters must needs result in a majority in the number of the stock, even if it had not been for the excess in temperature compared with that of our days, which was of course further contributing to an increase in the stock. In the Limfjord, the only one of our Danish waters in which a fairly large stock of oysters is living in our days, and where the conditions are somewhat similar to those of the Tapes age, the oyster is also rarely found in large numbers at quite low water ($^1/_2-1$ m). This is certainly due to the winter frost, as it freezes sometimes to the bottom in low water which the oyster cannot stand. It is, therefore, also to be supposed that during the Tapes age there was no such degree of freezing as in our days.

I am well aware that temperature and salinity are not the only determinative factors, as regards the distribution of the oyster. The distribution of the oyster in the northern waters, nowadays as well as in earlier periods, however proves that these two conditions, whether combined or apart, are of very great influence. Other conditions, nutrition, bottom quality a. s. f. may, of course, also be of importance, although certainly more locally. There can be no doubt that it is mainly the two first named factors which are decisive. In order to prove how great the importance of the quality of the bottom may be, I shall mention that no oysters are found in lower waters along the W. coast of Jutland, at the coast of the Aalbæk bay or at Læsø, no doubt on account of the loose sand bottom, although both temperature and salinity in these places are suitable to oysters. We have also seen that in localities where the temperature is the sole decisive factor, such as at the W. coast of Norway and in the deeper part of the Kattegat, the stock of oysters is constantly decreasing in accordance with the temperature, which is in good agreement with the mutual relation between temperature and spawning, stated by me in the above. Where the salinity is the decisive factor, as in certain localities in the Limfjord, the distribution is rather sharply limited. This appears very distinctly S. of Hvalpsund; there is namely a rather numerous stock of oysters in Risgaard Broad, Hvalpsund, and the northern part of Skive Fjord, but in the immediate neighbourhood, in Lovns Broad and the southern part of Skive Fjord, there are no oysters. Thus here we rather abruptly pass from an area with oysters in abundance to one with none at all. In this respect the cases in which the salinity, and those in which the temperature is decisive to the distribution, are clearly distinguished. The distribution fully confirms the great influence of the temperature on the spawning conditions of the oyster and also my conception of the nature of this influence, as described by me in the above. The distribution further very distinctly demonstrates that it is only in low and consequently warm water that the stock may become abundant, and that it is also in such localities (Arcachon, Ooster Schelde) that we may meet with the great opportunities for oyster fishing.

VI.

Theoretical Importance of Alternating Hermaphroditism.

Alternating hermaphroditism, the constant change between egg-developing and sperm-developing stages, not only is of consequence to our conception of the distribution of the oyster and of the fluctuations in the yield of the oyster fishing in the course of the years, it is also of some theoretical importance. Among the problems to which the demonstration of exactly this form of hermaphroditism is of some interest I shall here first mention the question about the hermaphroditism in the molluscs and the suggestions as to its origin. This problem was some time treated by Pelseneer (1894 p. 19). Through comparative morphological considerations he came to the conception that hermaphroditism in the molluscs was a secondary state whilst separate sexes were the primary, and that the hermaphroditism has originated through females in which a development of male products had begun. The hermaphroditic individuals thus are "genetic" females. Quite recently Goldschmidt (1920 p. 173) has, however somewhat doubtfully, put forth similar ideas, referring the hermaphroditism of the molluscs to the form of hermaphroditism which he indicates as unisexual monoecia. He makes, however, an exception as regards *Crepidula* which he refers to the group with the hermaphroditism, indicated by him as consecutive monoecia. According to Goldschmidt these latter hermaphrodites are males which are, on account of particular biological conditions (parasitism, sedentary mode of life a. s. f.), also developing into females. Thus the hermaphroditic individuals in certain *Crepidula*-species were to be "genetic" males. Finally Meisenheimer (1921 p. 59) introduces another point of view. He maintains that in many cases, among others as far as molluscs are concerned, it is impossible to speak of separate sexes and hermaphroditism as two stages which may be confronted as respectively primary and secondary or vice versa. According to Meisenheimer, the fact that species with separate sexes as well as hermaphrodites occur within one order of animals indicates the sex determination as not absolutely fixed, so that now one, now another of the two possibilities may be realized. An alternation of the kind, which I mean to have demonstrated in the oyster, seems to me completely to confirm the last named conception of the hermaphroditism in the molluscs. The fact that the two kinds of sex products are developed in the same follicles and that this development is, especially as far as the one sex is concerned, regulated by outer conditions, to wit, that of the temperature, is to me highly indicative of the sex not being so fixedly determined as is the case in many other groups of the animal world, wherefore both sexes are here developing in the same individual, according to the surrounding conditions. From this point of view there cannot be any discussion as to whether it is females or males which have become hermaphrodites, as in that case it would have to be both sexes which had become hermaphrodites.

If we examine the sex conditions in other molluscs we see (Pelseneer 1911 p. 101) that a great number of other Lamellibranchiata are hermaphrodites, and as a rule there are species with hermaphrodites as well as species with separate sexes to be found within the same groups. In numerous cases we are completely ignorant as to the nature of the hermaphroditism, for which reason it is impossible to have any opinion whether sex conditions similar to those in *Ostrea edulis* may be present in other Lamellibranchiata or not. In advance I should think it most probable. What is also of very great interest is the newly stated fact (Weisensee 1916 p. 262) that certain *Anodonta*-species become hermaphrodites when living in isolated, stagnant waters, but have separate sexes in water running. Weisensee even means to have proved that a stock having been isolated for a long time has become totally hermaphroditic, whilst only a small number of hermaphrodites were found in stocks having lived for a short time in stagnant water. The conditions of sex of the *Anodonta*-species seem to me to be in perfect agreement with the explanation given for the oysters. We have here beforehand an anything but fixed sex determination, wherefore an alteration in the surrounding conditions involves an alteration in the sexes mutually and in the development of the individuals separately.

If we leave the Lamellibranchiata and turn to the Gastropoda we here meet with similar conditions. In the Prosobranchiata we find the separate sexes to be prevailing, but a few forms are hermaphroditic, within a single species such as *Patella vulgata* we find both hermaphrodites and individuals with separate sexes. In Opisthobranchiata and Pulmonata it is, on the contrary, the hermaphroditism which predominates. In the last named the nature of the hermaphroditism in certain cases, f. inst. in *Limax maximus* seems to recall the sex conditions in the oyster (Babor 1898 p. 150). Besides in the Molluscs I have met with the report of a single case of hermaphroditism, apparently of a similar nature to that of the oyster, to wit in a Holothuria *Synapta inhærens* (Cuénot 1891 p. 623). In this species each sex period is said to be introduced by an egg-producing stage, followed by a sperm-producing one a. s. f., thus a similar process to that known from the oyster, only with proterogyny. No information is, however, given as to whether surrounding conditions have any influence on the length and development of the different stages, in this case. Possibly the rather complicated conditions of the hermaphroditism of an Asteroid, *Asterina gibbosa* (Cuénot 1898 p. 273), by which both females, males, and hermaphrodites are found together in certain localities, may be found out to be due to a similar alternation. Also as regards certain Ophiurids (Mortensen 1920 p. 1) this supposition may turn out to be correct. The occurrence of an alternating hermaphroditism thus may have its explanation in the fact that the sex determination is not in advance so definitely fixed that the influence of surrounding conditions on the realisation of the two constantly existing possibilities is excluded. This conception of the sex determination in these groups of animals is in no way contradicted by a study of further informations,

concerning the sex distribution in Gastropoda and especially in Lamellibranchiata. By means of these researches, any discussion of the hermaphroditic individuals as "genetic" males or females is further excluded. The male stage of the oyster being in northern waters by far exceeding the female stage, connected with the fact that the male stage is the first one, might indicate that the hermaphroditic oysters were to be regarded as males, which were also in a certain period developing eggs. It is a similar way of thinking which has led Goldschmidt (1920 p. 179) to consider the hermaphroditic *Crepidula*-species "genetic" males, whereby he becomes opposed to Pelseneer's conception of the hermaphroditic Molluscs, adopted by himself p. 173. The fact that a hermaphrodite commences as a male, or that the male stage prevails, does not mean that the animal "genetically" is a male. It only means that the development of the sexes is subject to the influence of certain conditions, to the effect that one sex may predominate, be the first or the like. Gould's experiments (1917 p. 1 and 225) with *Crepidula* clearly demonstrate such factors to be determinative. Hence the hermaphroditic Molluscs certainly include both males and females (neither males nor females would perhaps be the more correct expression) and when the two sex products are not developed simultaneously but in a certain consecutive order or alternation it is due to the influence of surrounding conditions, which is again to be referred to the "inner weakness" of the sex determination.

Through these reflections we have arrived at the problem of the origin of this hermaphroditism. Pelseneer (1894, 1911) has emphasized that the hermaphroditism is most frequently occurring in the so-called specialized species (parasites, sedentary forms, deep-sea forms, fresh-water forms) and he sees in this occurrence the confirmation of his opinion of the hermaphroditism of the Molluscs, as besides of hermaphroditism in general, to wit, as a secondary state which has been brought about through the fact that one sex may, on account of particular conditions, also develop the sex products of the opposite sex. That hermaphroditism is most often, though not always, occurring in species with deviating biology, only appears to me as an indication of the surrounding conditions as having influence on the sex-development. If a species living under certain conditions has developed separate sexes as a result of surrounding conditions and not of innate sex determination, an alteration in the surrounding conditions will, as a matter of course, involve an alteration in the sex development in the species in question, and we may expect a hermaphrodite to arise. In animals with a sex determination of the kind met with f. inst. in the Molluscs it is, therefore, to be expected that any alteration in the surrounding conditions, such as temperature, salinity, nutrition etc. may possibly involve an alteration from separate sexes to hermaphroditism. Weisensee's above named investigations of *Anodonta* as well as of the conditions of the oyster seem to me indeed the proof of this conception as being, in this case at least, the correct one.

Finally I shall only shortly mention another theoretical question to which

the hermaphroditism of the oyster may also be of some importance, i. e. the problem of sex determination itself. In comparison to the strong emphasis laid upon the importance of the morphologic elements (the chromosomes) against which the chemico-physical factors have been pointed out from other sides (Goldschmidt, Harms) as really effective, the conditions of the oyster appear to me to advocate the physico-chemical factors and not the morphologic. It is namely beyond all doubt that the development of the female sex is here to a high degree subjected to the regulation of the temperature in a manner which necessarily recalls chemical processes. Thus we have here one more instance, besides the already known *(Anuræ, Crepidula* a. o.) illustrating the decisive influence of the chemico-physical conditions on the development of the one or the other of the sexes.

VII.

Other Observations.

Finally I shall mention a certain number of observations concerning different sides of the biology of the oyster. I have made these observations more by chance during my stays at the Limfjord or in other ways during my investigations of the breeding habits. Only rarely I have had an opportunity to enter more closely on these observations. The reason why I now profit by the opportunity for publishing these observations here is that I imagine that some of these informations might be of interest to other naturalists, studying the biology of Lamellibranchiata, especially of the oyster. Another reason is that I intend through these, it is true, rather casual observations to put a sort of final stroke to the description of the biology of the oyster.

I shall first turn to the food and feeding habits. The in former days prevalent opinion that oysters as well as other Lamellibranchiata feed on plankton organisms is by now strongly shaken, even if it is still put forth. Already the demonstration by Redeke (1902 p. 103) that it was bottom diatoms which were found in the intestine of the oyster, was a blow to the previous conception. Also Rauschenplat (1901) and Lohmann (1908) in proving the great importance and distribution of the detritus further contributed to do away with the idea of plankton organisms as the food of the oyster. It is, however, only by C. G. Joh. Petersen (C. G. Joh. Petersen & Boysen Jensen 1911 p. 33) that we meet with a clear statement of detritus as an essential food source to the oyster, and this is further confirmed by Blegvad (1914) who refers the oyster to the feeders on detritus. Also Hoek (1912 p. 27) acknowledges that detritus may be of importance, at any rate besides the small bottom organisms. As a supplementary

remark to the discussion of the food and feeding habits of the oyster I shall state that under normal conditions it is always the detritus which constitutes by far the greater part of the contents of the stomach and intestine of the oyster. At different times of the year as well as in various localities in the Limfjord I have had an opportunity of examining the contents of the intestine of several hundred oysters, and in all cases the organisms, which were found in the intestine, were qantitatively completely insignificant compared with the detritus.[1]) As already proved by Blegvad (1914 p. 49) diatoms and *Prorocentrum micans* may pass alive and apparently quite unhurt through the intestine of the oyster. I have made just the same observation; in the rectum of the oyster I have found living Nematodes and Copepodes. The digestive secretion of the oyster thus seems to be of rather slight effect to several organisms. Only in a single case I have observed organisms to play a greater part in the contents of the stomach of the oyster, i. e. in the embanked Klovvig inlet in Venø. In the spring 1921, after the mouth of the inlet had been closed by an embankment, a certain number of oysters were laid out for the purpose of inducing oysters to better spawning here in the low warm water. After the embanking of the inlet had taken place the composition of the plankton, which had formerly been almost identic with the plankton of the Fjord, was rather considerably altered, enormous quantities of *Prorocentrum micans* were especially developed. In a number of oysters in the Klovvig *Prorocentrum micans* was so to say exclusively found in the intestine, during a period of the summer 1921. Later in the year oysters were found in the inlet with so to say no organisms in their intestines, but with nothing but a greenish mass of detritus, which is in good agreement with the fact that no number of organisms worth mentioning was found in the plankton of the inlet. That vegetable detritus, formed through the decade of algæ and *Zostera* leaves, is really of importance directly or indirectly to the feeding of the oyster I had further an opportunity of experiencing at the above mentioned aquaria experiments. For the feeding of the oyster I composed a sort of "artificial detritus", leaving *Fucus* and *Zostera* to putrify in bottles with sea-water, whereby was formed a greenish-brown amorphous mass, strongly recalling the detritus found in the intestine of the oyster. This artificial detritus I poured into an aquarium, in which I had for several months had oysters feeding on no other food than what might happen to be found in the aquarium, and the intestine of which had been proved through investigation to be empty; for further proof none of the characteristic mounds of excrements were accumulating round the animals. After this detritus had been added, it was, however, stated that the oysters, which were now opened, had the ordinary, greenly amorphous contents of the intestine, now totally free from organisms, except for the bacteria which may possibly be of importance in this connection, but of which

[1]) The recent investigations of *Teredo* (Potts 1923 p. 1) have led to results pointing in the same direction.

we are as yet completely ignorant. Oysters are very well capable of actively repulsing food (Wallengren (1905), Orton (1912)) wherefore the fact that these oysters took in this detritus certainly indicates that this latter is of some importance to their feeding and did not only by chance find its way into the intestine, as is often supposed by American authors (Lotsy, Moore)[1]. In this connection it further ought to be stated that an addition of carmine powder to the aquaria with oysters did not involve that carmine was found in any quantity worth mentioning in the intestine of oysters. Neither was it at all seasons that I succeeded in feeding oysters on the above mentioned detritus. In the months December-February it was impossible to make the oysters in the aquaria feed. This seems to me only to be comprehensible when we take into consideration that the oyster in the nature does not feed either at this time of the year. Already C. G. Joh. Petersen (C. G. Joh. Petersen & Boysen Jensen 1911 p. 33) have observed that oysters rarely appear to have any contents of the intestine in the winter. As said above, I have had an opportunity of seeing several oysters also in the winter and of examining their stomachs and intestines, and most often I have not found anything during the period from the last days of November to the middle of March. The only thing which can in the winter be pressed out of the rectum of the oyster are cells of epithelium and such like, the ordinary characteristic intestinal contents are wanting.

The point of time at which the oyster ceases feeding is somewhat varying, both as regards each year and each individual separately. The temperature seems to be of some influence here. In 1919 the oyster in the Limfjord ceased feeding already in the month of November, whilst in other years (the winter 1922—23) it still had contents in its intestine as late as about January. In 1919 the temperature of the water was in November especially low (below 0° C), whilst the winter 1922—23 was very mild. Food is once more found in the intestine of the oyster in the last days of March or the first days of April. But this does not occur to all oysters at the same date in the same locality. Of about 50 oysters which were examined $^{9}/_{4}$ 20 and which belonged to two localities in the Nissum Broad, only $^{1}/_{5}$ had contents in their intestines. In 1921 a few individuals with contents in the intestine were found $^{19}/_{3}$, after the middle of April so to say all individuals had these contents. The fact that the oysters in the aquaria did not feed in January—February, in spite of the high temperature, might indicate that the temperature is not the sole determinative factor in this connection, but that there is a certain periodicity dependant on inner factors which causes the animals, at any rate for a certain time of the year to be non-feeding. Further investigations are, however, needed in order to gain clear insight on this point; I have only mentioned it as

[1]) Also as regards the American zoologists it seems as if they are quite recently (Martin 1923 p. 143, Thurlow Nelson 1923 p. 90) becoming aware that the diatoms are of only small importance.

a not improbable possibility. Finally I shall call attention to the fact that at lower temperature oysters may live for a long time without any food at all, at any rate no kind of contents of the intestine is to be stated. I have, as said above had them in aquaria for 3—4 months without supplying any food to the aquarium, and without finding anything in their intestines. A single oyster which was forgotten in an aquarium lived there for $1^1/_2$ year without any food supply at all, a heap of *Mytilus* lying in the same aquarium lived for a few months more. The aquarium was placed in a room with no heating, the temperature was as a rule 7°—15° C. The intestine of Mytilus was now and then examined; each time the intestine appeared to be empty.

In connection with the food and feeding habits I shall say a few words about the crystalline style. The whole question of the crystalline style and the rather numerous theories put forth in explanation of its function have been most thoroughly treated by Thurlow Nelson (1918 p. 53), wherefore I shall not take it up for closer discussion. I shall only state as follows that the opinion, quite recently set forth by Berkeley (1923 p. 477), to wit, that the crystalline style is a reservoir of oxygen employed when the animals are exposed to lack of oxygen, does not appear to me to be well founded. It is especially totally opposed to observations made by me in the Limfjord. I have previously mentioned the oysters which were laid out in the summer 1922 in the embanked Klovvig, and of which all those in quite shallow water on the lee side died off in the course of the summer. These oysters were all lacking contents of their intestines and the crystalline style; but it cannot be the question of lack of oxygen in this case. The bottom and partly the shells of the oysters were namely densely covered by green algæ, the depth of the water also being very small (about 1 m), so that all possibility of lack of oxygen was excluded. The animals undoubtedly died for want of food, as said above. In this case the crystalline style thus has disappeared owing to lack of food, in spite of an ample supply of oxygen. Also on other occasions I have observed that a lack of food of long duration involves the disappearance of the crystalline style; as soon as the aquarium had been supplied with the above mentioned detritus, the crystalline style once more appeared in the oyster. The oysters which are found in the winter in the nature without any contents in their intestines are likewise destitute of crystalline style. On the other hand, a lack of food of short duration does not result in the disappearance of the crystalline style. Oysters which have been lying dry, which always involves that the crystalline style disappears, redevelop this latter when they are put down in an aquarium, even if there is no food present. If the lack of food is continued the style again disappears. All this serves to prove that in some way or other, perhaps in many ways, there is a certain connection between the crystalline style and the food and feeding habits of the oyster, such as already the position of the crystalline style in the intestine might suggest. It seems at present impossible to state with certainty of what nature this connection is. I shall only mention two facts con-

cerning this matter. One is that in confirmation of Thurlow Nelson's observation of the rotation of the crystalline style I can state having found the crystalline style in the oyster with the mass of detritus wound spirallike round the style. I can further maintain that, according to my experience, the crystalline style is always lacking when, for some reason or other, there is anything amiss with the oyster. In winter when the death rate has been high, owing to the cold, in summer when the same thing occurs, on account of the heat, when food is wanting, when the animal lies dry, when it is infected, in every single case the crystalline style is lacking. It is, therefore, my opinion that the absence of the crystalline style must be interpreted as an indication of something not quite normal, as regards the state of metabolism and nutrition, a. s. f. It is of practical importance that information of the "state of health" of a stock of oysters (f. inst. in a basin or the like) can always be obtained by opening some of them and examining whether the crystalline style is present or not.

The question of the death rate of the oyster has been discussed by me in the above, and I have mentioned that I had the impression that it was rather high in the Limfjord, as besides probably everywhere. This is, among other things, connected with the great number of enemies which the oyster has. Of the series of enemies which may, according to the synopsis by Dollfus (1921), attack adult oysters, there are, however, only two which are of greater importance in the Limfjord, namely the common Asteroid (*Asterias rubens*) and the common crab (*Carcinus mænas*). I never had the opportunity of seeing *Asterias rubens* attack an adult oyster, whereas I have had direct proof of the violence with which the crabs may set to work. In the summer 1919, 13 oysters, the greater part of which with the above mentioned holes bored in their flat shells, were set out by me in a small basin, only separated from the surrounding Fjord by perforated woodwork. On the following day, when I came to inspect the before named 13 oysters, I found the basin filled with crabs, whilst there was nothing left of the oysters, except for the empty shells, in which not even the least remnant of the animals was to be seen. The shells wore distinct marks of the crabs having worked upon them with their chelæ, the above mentioned small holes had in some cases been rather considerably widened, sometimes a triangular notch had even been cut in the shell margin. This observation indicates that the common crab is capable of making an anything but insignificant inroad on the stock of oysters. It was likewise most interesting, on the following day, to see more than 20 *Asterias rubens* advancing towards the basin. This indicates that these animals are for some reason or other conscious of the presence of oysters at a distance, and that oysters attract *Asterias rubens*, which rather suggests that oysters are of importance as food stuff to the Asteroids. Of the numerous parasitic sufferings, which Dollfus enumerates with reference to the oyster in his above named synopsis, I have only observed a few in the Limfjord, to wit, the so-called "maladie du pied" and they even appear to be rather rare, and *Polydora* sp. and *Clione celata* which are only met with in the

western part of the Fjord and are seemingly of no particular importance. *Clione celata* besides only attacks older oysters, just as *Polydora* which is only seen now and then and, therefore, cannot be thought to have any influence worth mentioning on the death rate of the oyster. It is not the parasitic sufferings, which are, as an essential factor, besides the crabs and perhaps the Asteroids, contributing to the mortality of the oyster, at any rate not in the Limfjord, but another peculiar state of weakness which manifests itself in the oyster not being able to close its shells, the muscle having somehow been paralysed. All sorts of transitions are to be observed from totally normal, animals, being able to close their shells quite tight, through some which are only feebly reacting to irritation, as f. inst. from blows or stabs, to such, which do not react at all, even if they are taken out of the water and a needle stuck into their muscle; the shells cannot even be closed, they at once reopen, if they are pressed together. The animals do not die, even in the last named case they are not dead; if they are pricked in the margin of the mantle it will be seen that it moves, and the animals are not immediately putrifying. Another thing is that these animals, of course, rapidly become a prey to crabs, Asteroids, a. s. f., and that the muscle is gradually atrophied. The suffering, however, ceases if the cause is removed. The suffering is not always due to the same cause, and this paralysis of the muscle seems to be the symptom of different sufferings, exactly as the disappearance of the crystalline style. The paralyses may be brought about through lack of food under high temperature; if in such a case food is supplied, the paralysis ceases, even if it has been present in a rather high degree. Similar observations may be made, if the paralysis occurs at a great refrigeration of the water. If the water is for a longer time cooled down to below $\div$ 1,5 ^{0} C exactly the same state sets in. In aquaria it may, however, be abolished through heating the water. In the winter 1919—20 the death rate of oysters, taken in the inner part of the Limfjord, was, as mentioned in my previously quoted report, anormally high at a certain period, even on account of the occurrence of such a state having been brought about through the very low temperatures in November 1919. The anormally high death rate, ravaging the stock of oysters in W. Europe in 1920—22, especially in 1921, seems to have its cause in the very same paralysis of the muscle (Orton 1923 p. 1). At any rate no parasite or any other similar common cause have been found out. What has provoked the paralysis is apparently unknown; I might suggest lack of food, on account of the high temperature which is in 1921 said to have predominated in the English waters, thus something quite corresponding to what I observed on a smaller scale in the Klovvig and in aquaria. This death rate of W. Europe in 1921 is however, according to Orton, not to have been so extremely high as it has been maintained from certain parts. Any especially striking general death rate has not been observed in the Limfjord these last years.

The growth of the oyster in the Limfjord has, as said above, already been thoroughly treated by C. G. Joh. Petersen (1907 & 1908), and I shall, therefore, only slightly mention this question. I shall f. inst. state that the Dutch oysters,

relaid in the Nissum Broad, were during the first summer increasing in average size from 5—6 cm to 6—7 cm; in the second summer they reached a size of 7—8 cm, some few even of 9 cm. They were then a little more than 3 years old. In my report from 1921 I have emphasized that the oyster does not increase in size with equal rapidity in all parts of the Fjord, and that this fact is evidently in relation with the difference in salinity. In the part of the Fjord with the lowest degree of salinity, to wit Risgaard Broad, even an old oyster never becomes more than 10 cm in size, and the average size is of 7—8 cm. In Thisted Broad with an a little higher salinity the maximum is about 12 cm, the average about 9—11 cm, in the Livø Broad the maximum is 13 cm, the average 9—11 cm, also in the Nissum Broad we have this average size, but here we meet with oysters obtaining beyond 15 cm in size in the most western part with the highest salinity. Such a correlation between salinity and size is of importance, not only for the purpose of estimating the age of an oyster by means of its size, but from the maximum and average size of the oyster it is possible to form an approximate opinion of the salinity of the water in question. Some attempt like this might f. inst. be made with reference to the sea of the Stone Age.

I shall now make a few finishing remarks concerning the so-called "green" oysters. This phenomenon, which has previously been observed in a basin at the Limfjord (C. G. Joh. Petersen 1914 p. 39), appeared for the first time in the very Limfjord in the autumn 1921. It was reported in the month of September from a limited area at Lemvig Røn in the Nissum Broad. It disappeared in the course of the winter. I shall not render any special account of the rather heated discussion which has been raging about this question, as it has been exactly reported by, among others, Carazzi (1897 p. 381) and Sauvageau (1907 p. 1). The new observation, which I have to introduce is that not only the oysters but also a whole series of other animals, such as *Mytilus edulis, Corbula gibba, Asterias rubens* turned green. In the oysters as well as the other Lamellibranchia it was the gills which turned green, in the Asteroids the ends of the tubefeet. Another peculiarity of interest was that the green colour, which disappeared rather rapidly in the oyster, was constant for a couple of years in *Asterias*. It was likewise found in *Asterias* but not in oysters, in other localities in the Limfjord. This latter fact seems to me to refute the theory of the green colour as being due to diatoms in the food of the oyster. First of all it appears that the diatoms are of scanty, not to say no importance at all, to the food of the oyster, and then it is excluded that *Asterias rubens* should be feeding on diatoms. That the green colour should derive from a precipitation in the above named tissues of certain substances in the water cannot easily be made to agree with the sporadic, local occurrence of the colour in a water with frequent currents as the Limfjord. Thus I was induced to think that the green colour might possibly be due to intracellular parasites of a similar kind as those stated by Pierantoni, Buchner a. o. to occur in a series of animals. For the purpose of demonstrating the parasite some experiments were kindly made

at the State Institute of Serology by Dr. m. Ørskov, without, however, refuting or confirming the supposition. Still it is a fact that the green gills are much more rapidly putrifying than the not green. The sudden occurrence in certain very limited localities in the Fjord also seems to me to indicate a parasite to be the true cause. Continued but not yet concluded researches on material from France have at any rate proved the phenomenon, so suddenly appearing in the Limfjord in 1921, as exactly corresponding to the one which is normally occurring at Marennes and in other localities at the coasts of France.

VIII.

Conclusions.

I shall now finally recapitulate some of the most important facts and views of this paper in the following statements:

1. The temperature is of special importance to the breeding habits of the oyster in two respects, a high temperature results in an increase in the production of spawn and propagates the growth of the pelagic larvæ, which has again for result that a greater number of larvæ live through the pelagic stage.
2. The oyster is a protandric alternating hermaphrodite, the sperm-producing period is followed by an egg-producing, and this again by a sperm-producing a. s. f. The genital products, which are not getting into function in the present summer, may be utilised in the next breeding period.
3. The influence of the temperature on the production of fry is due to this very form of hermaphroditism as the egg-development is forwarded by the high temperature, whilst it becomes the slower, the lower the temperature, till it practically ceases at 10°—12° C. At temperatures about 20°—22° C each individual oyster may become a female once a year, at temperatures about 14°—16° C every 3—4 year, at lower temperatures still more rarely, and at last not at all. This is in good agreement with the fact that the warmer it is, the younger the oyster is when it commences producing eggs. At S. France in the first year, in the Limfjord as a rule only in the third or fourth. The warmer it is, the shorter will be the interval between the times when an oyster produces eggs, and the more abundantly the stock will be increased.
4. These latter facts, therefore, serve to explain the fact that in cold waters such as the deep Kattegat and at the W. coast of Norway the stock of oysters is much more scanty than in the Limfjord. Where the temperature is the limiting factor to the distribution of the oyster, it will consequently be decreasing smoothly in number, till at last it disappears. The boundary line will not be

distinct, as it is in places where the salinity is the most important limiting factor. It namely appears that oyster larvæ cannot complete their growth in water with a salinity of below 24—25 ‰.

5. The occurrence of a fixed temperature limit, above which all oysters and below which no oysters should be spawning, is perfectly excluded. There exists no such definite distinction between good and bad spawning years, but every possible transition according to the height of the temperature. No fixed height of temperature is needed in order to make an oyster attach itself; even in the coldest summers in the Limfjord with only 13°—14° C a few larvæ attach themselves. A decrease in temperature and salinity does not immediately have a mortal effect on the larvæ, their growth is simply checked or brought to a close.
6. The above named form of hermaphroditism, in connection with other informations concerning similar conditions in the Mollusca *(Anodonta, Crepidula, Patella vulgata)* indicate that the inner sex determination is here but slightly fixed in advance, hence surrounding conditions become of regulating influence to the development of the sexes. An alteration in the surrounding conditions, therefore, results in an alteration in the kind of the sex, as is the case in f. inst. *Anodonta*, according to Weisensee.
7. It is confirmed that the detritus of plants is of importance to the nutrition of the oyster. In aquaria oysters will take in detritus of plants free from organisms, except for the bacteria. The crystalline style is in relation with the nutrition and cannot be a reservoir of oxygen. Its presence or absence is a symptom of the state of the oyster being normal or not.
8. The death-rate of the oyster in the Limfjord seems to be about 20 % of the stock yearly. One of the most noxious animals to the stock of oysters in the Limfjord seems to be the common crab *(Carcinus mænas)*. Parasitic sufferings appear on the other hand to be of small importance. Of great consequence is, besides, the paralysis of the muscle preventing the muscle from contracting, which is, among other things, caused by an abnormally high or abnormally low temperature or through lack of food. The animal does not die at once, but soon becomes a victim to carnivorous animals or infections.
9. In the autumn 1921 more than 90 % of all oysters in a certain locality in the Limfjord had green-coloured gills. It turned out to be exactly the same phenomenon as that occurring at Marennes. Not only oysters in which the phenomenon disappeared in the course of the winter were attacked, but also a series of other animals, partly different Lamellibranchiata, partly *Asterias rubens*, of which the ends of the tubefeet were green, and in which the phenomenon lasted for a certain length of time. The conditions in the Limfjord indicate that the cause of this phenomenon is to be sought in the attack of an intracellular parasite.

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* indicates papers not seen by me but which I know from quotations.

POSTSCRIPTUM.

Some time after having finished this paper, which was printed in Danish in the spring and summer 1924, I became acquainted with two treatises which I regret not having met with early enough for using during the working out of my paper. They are: I. H. Orton: Sex Change and Breeding in the Native Oyster, O. edulis (Nature Vol. 114 1924, p. 191) and by the same author: An Account of Investigations into the Cause or Causes of the unusual Mortality among Oysters in English Oyster Beds during 1920 and 1921 I—II (Fish. Investig. II Vol. 6 1924). In these two papers some of the facts, discussed in my paper are treated. Of special interest is the demonstration of the change from female to male, to which result the author has come by the same method as used by me at my investigations in 1919, and by which my observations (p. 31) are perfectly confirmed.

IX. Trawlings in the Skager Rack and the Northern Cattegat in 1897 and 98. 1899. 56 pg. With one Map.

X. Fortegnelse over Aalerusestader i Danmark etc. — Mindre Meddelelser. 1899 og 1900. 36 pg. Et farvetrykt Kort. (1900—01.)

X. List of The "Aalerusestader" in Denmark, etc. — Smaller Communications. 1899 and 1900. 37 pg.

XI. I. Torskens Biologi i de danske Farvande. II. Om andre Torskefisk i vore Farvande. III. Nogle almindelige Betragtninger om Fredning, Lovgivning etc. IV. Ændringer og Forbedringer af Skovlvaad til zoologisk Brug. 44 pg. (1900—01.)

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